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THE UNIVERSITY OF ALBERTA

Morphology and Systematics of Primitive Simuliidae
(Diptera: Culicomorpha).

by

Douglas C. Currie

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF Doctor of Philosophy

Entomology

EDMONTON, ALBERTA
Fall 1988

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Morphology and Systematics of Primitive Simuliidae (Diptera: Culicomorpha) submitted by Douglas C. Currie in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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External Examiner

Date 10 - x - 88

To my father

ABSTRACT

This thesis is comprised of two papers: "A phylogenetic interpretation of the primary evolutionary lineages of Simuliidae (Diptera: Culicomorpha)"; and "Monophyly and relationships of genus-group taxa of Prosimuliini (Diptera: Simuliidae)". In the first chapter, the monophyly and sister-group relationship of Simuliidae are discussed, and simuliid groundplan characters reviewed. Twenty-three characters or character systems are hypothesized as probable synapotypies of the family. Analysis of all life-history stages of *Parasimulium* Malloch *s.lat.* provides phylogenetic resolution of the earliest lineages of Simuliidae. Based mainly on features of the immature stages, a sister-group relationship is suggested between *Parasimulium s.lat.* (= Parasimuliinae) and all other Simuliidae (= Simuliinae). Thirteen hypothesized synapotypies are given in support of the monophyly of Parasimuliinae, and 15 synapoptypies in support of the monophyly of Simuliinae. Within this latter clade, the initial dichotomy is as follows: Prosimuliini (*Prosimulium* Roubaud, *Helodon* Enderlein, *Parahelodon* Peterson, *Distosimulium* Peterson, *Urosimulium* Contini, *Levitinia* Chubareva & Petrova, *Twinnia* Stone & Jamnback, and *Gymnopais* Stone), and Simuliini (all other Simuliinae). Five hypothesized synapotypies are provided for each of the 2 tribes. Resolution of the primary lineages of Simuliidae permits interpretation about the zoogeography and early evolutionary history of the family. The advantages of a classificatory system based on phylogenetic relationships are discussed. In the third chapter, eighty-one apotypic character states or character systems of larvae, pupae and adults are analyzed for evidence of monophyly and phyletic relationships of genus-group taxa of Prosimuliini. The following monophyletic genus groups are recognized, based on 2 or more hypothesized synapotypies each: *Prosimulium* Roubaud *s.str.* (66 species), *Helodon* Enderlein *s.str.* (13 species), *Parahelodon* Peterson (3 species), *Distosimulium* Peterson (2 species), *Urosimulium* Contini (3 species), *Levitinia* Chubareva & Petrova (2 species), *Twinnia* Stone & Jamnback (10 species), and *Gymnopais* Stone (12 species).

Most previous concepts of *Prosimulium s.str.* and *Helodon s.str.* are shown to consist of non-monophyletic assemblages of species. *Prosimulium s.str.* is hypothesized to be the monophyletic sister taxon of all other Prosimuliini. Three major lineages are recognized within this latter assemblage as follows: (1) *Helodon s.str.*, (2) *Parahelodon* + *Distosimulium*, (3) *Urosimulium* + *Levitinia* + *Twinnia* + *Gymnopais*. Analysis of structural characters alone does not resolve relationships among these three clades. The partially resolved cladogram provides the information necessary to "root" published reconstructed cytological transformation series ("cytophylogenies"), which are derived from unrooted, hypothetical, "standard sequences" (e.g. Rothfels 1979). The resulting topology is used to test hypotheses about relationship, and to provide resolution where structural information alone has failed. This combination of morphological and cytological information yields a reconstructed phylogeny, providing the basis for a reclassification of Prosimuliini. The following system of genera and subgenera is adopted: *Prosimulium*, *Helodon s.lat.* (including the subgenera *Helodon s.str.*, *Parahelodon*, and *Distosimulium*), *Urosimulium*, *Levitinia*, *Twinnia*, and *Gymnopais*. The nominate subgenera *Parahelodon* and *Distosimulium* are relegated in new status from *Prosimulium s.lat.* to *Helodon s.lat.* A check list of world species of Prosimuliini is arranged according to the new classification, with 24 species relegated in new combination. Keys to larvae, pupae, and adults of genus-group taxa of Prosimuliini are provided.

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1. INTRODUCTION

If biological classifications are systems of words that are used to organize the diversity of life and/or to reflect man's estimate of nature's own organization of life (Wiley 1981), then the process of biological classification must be a very ancient phenomenon indeed. There can be little doubt that the earliest words uttered by man included reference to the flora and fauna surrounding him. Biological classifications serve as an information storage-and- retrieval system, and their construction remains one of the fundamental tasks of the modern-day systematist.

Aristotle provided the first significant attempt at a division of the Animal Kingdom into "Classes", by distinguishing "Animals that have blood" (Viviparous quadrupeds, Oviparous quadrupeds, fishes, birds) and "Animals that have no blood" (Molluscs, Crustaceans, Testaceans, Insects) (Lamarck 1914). In essence, the first mentioned Class is defined by a shared derived character —a synapotypy— whereas the second Class is defined by the lack of that character, or by some contrasting character (a symplesiotypy). Eldredge and Cracraft (1980) refer to such assemblages as "A groups" and "not-A groups", respectively. Not-A groups are rejected in a cladistic system because assemblages that are defined on the basis of symplesiotypy are generally unnatural or non-monophyletic.

Despite advances in the application of phylogenetic principles *sensu* Hennig (1966), divisions based on A and not-A groups have dominated classificatory systems since the time of Aristotle. Classic examples of not-A groups include "Vermes" (worm-like animals) and "Invertebrata" (animals that lack a back bone). Although such groupings are still widely recognized, the history of biological classification shows that there is a tendency towards elimination of not-A categories. This process is aided through a more thorough understanding of character systems, and stricter application of phylogenetic techniques.

Present-day classifications of black flies (Diptera: Simuliidae) still are organized largely into systems of A and not-A categories. This is in no way intended as a repudiation of the efforts of earlier workers, as black flies are notorious for their structural homogeneity. Moreover, until very recently, there was a basic lack of information about some key plesiotypic members. In the absence of convincing evidence about phylogenetic relationships, the convenient but unnatural classification served its purpose for day to day communication about black flies.

Although "convenience" or "compromise" classifications have served their purpose leading into the Twenty First century, there are signs that specialists are becoming less satisfied with the large number of unnatural groupings currently recognized in Simuliidae. Wygodzinsky and Coscarón (1973) maintain that a clear-cut division of the tribes Prosimuliini and Simuliini (at least as currently recognized) cannot be upheld in a cladistic system. Prosimuliini is a classic example of a not-A assemblage, because it is defined on the basis of lack of those characters (or by contrasting characters) that define Simuliini.

Cytotaxonomy, the study of giant, polytene, larval, salivary gland chromosomes, has provided convincing evidence about relationships at the genus-group level (Rothfels 1979, 1987). Such investigations have caused the morphotaxonomist to rethink seriously conclusions based on *a priori* assumptions about the direction of character evolution. Similar advances are being made with other "non-traditional" techniques as well. For example, DNA: DNA hybridization, gas liquid chromatography, and electrophoresis have all provided fresh insights about the relationships of black flies (see Crosskey 1987, and Townson *et al.* 1987 for reviews). Although the full potential of these techniques has yet to be realized, it is clear that cytotaxonomic- and chemotaxonomic endeavors will continue to raise pertinent questions about present-day classifications of Simuliidae. There is thus an uneasy relationship between the practical needs for a classification (taxa definition, identification), and the desire for a system that accurately reflects phylogenetic relationships (Crosskey 1987).

Evidence is accumulating that there can be close agreement between phylogenies derived from morphological and cytological information if characters are viewed in a cladistic framework. In Chapter 3, for example, a phylogenetic interpretation of Prosimuliini genus-group taxa almost exactly reflects published cytophylogenies for the same groups. Craig (1983) has found similar results in his investigation of Polynesian Simuliidae, stating: "A reconstructed phylogeny, based mainly on morphological character states of larvae and pupae, agrees well with the cytophylogeny". Knowledge about the family is now at a stage where the gap between classification and phylogeny can be narrowed.

The intent of this thesis is to investigate phylogenetics and classification of the most primitive lineages of black flies. In Chapter two, structural features of all life-history stages of black flies are analyzed for evidence of monophyly and sister-group relationships of the primary evolutionary lineages of Simuliidae. This analysis was made possible through discovery of the female and immature stages of *Parasimulium* Malloch — a genus that was hitherto known only from the male. *Parasimulium* has been considered the most primitive simuliid, based on several unique features of the head and terminalia of the adult male. Results of this analysis provide the basis for a suprageneric classification of Simuliidae, based on phylogenetic relationships.

In Chapter three, I focus on one of two major lineages recognized in the subfamily Simuliinae — the tribe Prosimuliini. Characters of larvae, pupae, and adults are analyzed for evidence of monophyly and phylogenetic relationships of the eight genus-group taxa recognized in that tribe. The resulting cladogram is used to "root" published cytological transformation series of the same taxa. This combination of morphological and cytological information yields a well-corroborated reconstructed phylogeny, providing the basis for a reclassification of Prosimuliini.

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2. A PHYLOGENETIC INTERPRETATION OF THE PRIMARY EVOLUTIONARY LINEAGES OF SIMULIIDAE (DIPTERA: CULICOMORPHA).

2.1 Synopsis

The monophyly and sister-group relationship of Simuliidae are discussed, and simuliid groundplan characters reviewed. Twenty-three characters or character systems are hypothesized as probable synapotypies of the family. Analysis of all life-history stages of *Parasimulium* Malloch *s.lat.* provides phylogenetic resolution of the earliest lineages of Simuliidae. Based mainly on features of the immature stages, a sister-group relationship is suggested between *Parasimulium s.lat.* (= Parasimuliinae) and all other Simuliidae (= Simuliinae). Thirteen hypothesized synapotypies are given in support of the monophyly of Parasimuliinae, and 15 characters in support of the monophyly of Simuliinae. Within this latter clade, the initial dichotomy is as follows: Prosimuliini (*Prosimulium* Roubaud, *Helodon* Enderlein, *Parahelodon* Peterson, *Distosimulium* Peterson, *Urosimulium* Contini, *Levitinia* Chubareva & Petrova, *Twinnia* Stone & Jamnback, and *Gymnopais* Stone), and Simuliini (all other Simuliinae). Five hypothesized synapotypies are provided for each of the 2 tribes. Resolution of the primary lineages of Simuliidae permits interpretation about the zoogeography and early evolutionary history of the family. The advantages of a classificatory system based on phylogenetic relationships are discussed.

2.2 Introduction

Black flies (Diptera: Simuliidae) form a compact, easily recognized family of nematocerous Diptera. About 1450 species are known world wide, with representatives in all continents except Antarctica (Crosskey 1981b, 1987). The number of undescribed species is probably considerable, because many sibling species are found in what are inferred (on external structural grounds) to be single reproductive entities (see Rothfels 1979, 1981, 1987 for reviews). But despite our incomplete knowledge about sibling species on a world-wide scale, it is probable that most of the structural divergence of Simuliidae has already been documented.

While the Simuliidae as a whole is very easily recognized, and its relationships with other Nematocera reasonably well established (*e.g.* Hennig 1973, Wood 1978), relationships within the family have remained somewhat obscure. The difficulty in part lies with an almost uninterrupted sequence in form between plesiotypic and more apotypic members (Crosskey 1973). Another problem is incomplete knowledge of the life history stages of certain plesiotypic taxa. This latter has frustrated attempts to polarize certain key character states, particularly those of the immature stages. Black flies are few in the fossil record, and those that have been described shed little light (Crosskey and Taylor 1986). In the absence of a complete fossil record, notions about the evolutionary history of Simuliidae will have to be inferred from the extant fauna.

The most primitive extant simuliid is generally believed to be *Parasimulium* Malloch, a genus that is currently only known from the western-most United States (Peterson 1977). The primitive status of *Parasimulium* has largely been inferred from the wing venation, which has R_1, R_{2+3}, and R_{4+5} widely separated at the costa (these veins are more crowded in other simuliids). This, and several unique features of the head and terminalia have led most workers to recognize a separate subfamily for members of the genus (*e.g.* Smart 1945, Shewell, 1958, Grenier and Rageau 1960, Dumbleton 1963, Crosskey 1969, Rubtsov 1974, Peterson 1977). Interpretations prior to 1981 were all based on the adult male as this was the only stage known. In fact, until 1981, only 8 male specimens had been collected in total, comprising 2 subgenera and 4 species: *Parasimulium s.str.* (*P. furcatum* Malloch, *P. crosskeyi* Peterson, and *P. stonei* Peterson) and *Astoneomyia* Peterson (*P. melanderi* Stone) (Peterson 1977). The only modern worker not according subfamilial rank to *Parasimulium* was Stone (1963, 1965), who instead reconized the tribe Parasimuliini within the subfamily "Prosimuliinae".

Because of the apparent primitive status of *Parasimulium*, many efforts have been directed at collecting the female and immature stages. It was generally agreed that the phylogenetic position of *Parasimulium* could only be established in view of all life-history stages. But despite repeated attempts to obtain additional material, a period of 46 years passed between the last collection of *Parasimulium* (in 1935), and the re-collection of *P. crosskeyi* in 1981 (Wood and Borkent 1982). This latter discovery was particularly important because, as well as significantly adding to the number of known male specimens, the female of *Parasimulium* was collected for the first time.

Using both male and female characters Wood and Borkent (1982) reassessed the phylogenetic position of *Parasimulium*, and with cladistic techniques proposed a sister-group relationship between that genus and all other Simuliidae (Fig. 3 a). This supported the notions of most previous workers whose conclusions were based on a non-cladistic or dialectical approach to systematics. Characters given in support of the monophyly of *Parasimulium* included: (1) reduction of katepisternum, (2) loss of mesepimeral tuft, and (3) loss of peglike seta at apex of gonostylus. Synapotypic characters given for Simuliidae exclusive of *Parasimulium* included: (4) eye of male with line of discontinuity between large upper and small lower facets, (5) crowding of branches of radial sector (R_{2+3} and R_{4+5}), and (6) sternum 10 of female divided. This evidence was given in support of a two-subfamily arrangement for Simuliidae, in which Parasimuliinae comprised *Parasimulium* and Simuliinae comprised all other simuliids (Wood and Borkent 1982).

More recently these same authors (Borkent and Wood 1986) obtained first- and second-instar larvae of *Parasimulium stonei* from eggs laid *in vitro*. This material provided additional information by which their original hypothesis, based on adult characters alone, could be tested. But instead of corroborating their earlier hypothesis, larval characters suggested a close relationship between *Parasimulium* and some typical members of the Prosimuliini *sensu* Crosskey (1969) (Fig. 3 b). This lent support to the classifications of Stone (1963, 1965), in which *Parasimulium* was considered merely an aberrant side branch of the tribe Prosimuliini. The primary character given in support of this relationship was loss of the labral fan in first-instar larvae. On this basis, *Parasimulium* was presumed to have shared an immediate common ancestor with *Crozetia* Davies, *Prosimulium* Roubaud, *Gymnopais* Stone, and *Twinnia* Stone & Jamnback. In view of the conflict between larval and adult apotypies, it is clear that other characters will have to be examined to determine the relationship of *Parasimulium* to other simuliids (Borkent and Wood 1986).

Courtney (1986) recently reported discovery of later-instar larvae and pupae of *Parasimulium crosskeyi*, and provided brief descriptions. In this chapter I redescribe this material, evaluate its character states, and provide for the first time an analysis based on all life-history stages of *Parasimulium*. This analysis tests the conflicting hypotheses based on larval (Borkent and Wood 1986) and adult (Wood and Borkent 1982) characters alone. In addition to further resolving the relationship of *Parasimulium* to other black flies, I offer an initial cladistic interpretation of the primary evolutionary lineages of Simuliidae.

2.3 Taxonomic history

The taxonomic history of Simuliidae begins with the publication of *Systema Naturae* (Linnaeus 1758), although antecedent man was undoubtedly familiar with anthropophilic forms. While it is beyond the scope of the present study to review all taxonomic works dealing with the higher classification of the family, it is nonetheless relevent to provide a review of some of the more important contributions. Smart gave a detailed review of works to 1945. Reviews of later works have been provided by Rubtsov (1974) and Crosskey (1981a). The following taxa are central to understanding the early evolutionary pathways of Simuliidae, and so special emphasis is placed in this section on the timing of their discovery, and the role their discovery played in shaping present-day notions about classification: *Parasimulium* Malloch, *Prosimulium* Roubaud *s.lat.*, *Twinnia* Stone & Jamnback, *Gymnopais* Stone, *Procnephia* Crosskey *Paracnephia* Rubtsov, and *Crozetia* Davies. The first section is a brief account of some classificatory schemes proposed to date. This is followed by a section about other contributions or discoveries which have had a bearing on notions about phylogenetic relationships.

2.3.1 Higher Classification

Linnaeus (1758) placed the first described simuliids (*reptans* L., *equinus* L.) in the culicid genus *Culex*. The distinctiveness of black flies went unrecognized until 1802, when Latreille established the genus *Simulium* to accomodate all the species known at that time. Thirty-two years later, the taxon "Simulites" was created by Newman (1843), providing the modern-day basis of the family name. Apart from scattered species descriptions, the state of simuliid classification remained unchanged from this point until the present century.

Until the early 1900's all described simuliids (30-40 species) were relegated to the genus *Simulium* Latreille. The first step towards recognizing simuliids as a polybasic group was taken by Roubaud (1906) who distinguished — primarily on details of the hind leg — two subgenera in *Simulium* ("*Pro-simulium*" and "*Eu-simulium* "). These were ranked along with *Simulium s.str.* as full genera within five years by Surcouf and Gonzalez-Rincones (1911).

The taxonomic significance of the wing was first recognized by Malloch (1914) who distinguished, on features of the radial sector, *Prosimulium* (R_s forked) from *Simulium* (R_s unforked). Another of Malloch's contributions was the description of the genus *Parasimulium,* which was characterized by several unique features of the eyes (widely separated at vertex, occurrence of larger-sized facets near middle of eye) and wing (absence of a basal medial cell). Although the original description was based on a single specimen, its features seemed distinctive enough to warrant generic recognition. The distinctiveness of *Parasimulium* was magnified even further by the discovery that the specimen was a male, and not a female as originally described (Knab 1915). The vast majority of simuliid males are holoptic, and their eyes have a distinct line of separation between the large upper facets and the small lower facets. Ironically Malloch failed to note one of the most conspicuous features of *Parasimulium,* which is the widely separated branches of the radial sector.

The *status quo* in simuliid classification prevailed until the 1920's, when a multitude of supraspecific names was introduced. This was due almost entirely to the efforts of a single German worker — G. Enderlein. In the interval between 1921 and 1937 no less than 23 papers were published (Enderlein 1921 *et seq.*), in which 50 genera were recognized (most described by Enderlein himself). Moreover, Enderlein was the first worker to erect a suprageneric classification of Simuliidae. In his apparent final work on the family, Enderlein (1937) recognized a total of 7 subfamilies and 5 tribes: Prosimuliinae, Ectemniinae, Cnesiinae, Stegopterninae, Nevermanniinae (Nevermanniini, Friesiini, and Wilhelmiini), and Simuliinae (Simuliini and Odagmiini). Remarkably, in that work he was either unaware of, or chose to ignore, the work of Malloch, for no mention was made of *Parasimulium.*

Edwards, a contemprary of Enderlein, forwarded a radically different classificatory scheme. In his final attempt at a classification, Edwards (1934) recognized but two genera of black flies: *Parasimulium* Malloch and *Simulium* Latreille. Five subgenera were delimited in the latter genus: *Prosimulium* Roubaud, *Cnephia* Enderlein, *Gigantodax* Enderlein, *Austrosimulium* Tonnoir, and *Simulium* Latreille. No attempt was made at a suprageneric classification of the family.

Smart (1945), in recognizing the need for a clear monographic account of the family, provided a critical analysis of both Enderlein's and Edwards' work. He criticized the former author for disregarding the treatments of other taxonomists, for his use of spurious structural characters, and for his failure to consider both male and female characters. These deficiencies contributed toward an overestimation of supraspecific taxa. Of Edwards' work, Smart cited a failure to define phylogenetically significant characters, with too few genera being recognized as a result. As an alternative Smart proposed that simuliids be organized into a system of six genera and two subfamilies. *Parasimulium* Malloch was to be isolated in its own subfamily (Parasimuliinae), and *Prosimulium* Roubaud, *Cnephia* Enderlien, *Gigantodax* Enderlein, *Austrosimulium* Tonnoir, and *Simulium* Latreille were to be united in another (Simuliinae). No tribes or subgenera were recognized. Although Stone (1941) was the first to describe the widely branched radial sector of *Parasimulium,* it was Smart who interpreted the condition as being plesiotypic within Simuliidae. This is the foundation upon which most subsequent classifications are based, for the degree to which the radial sector is branched is one of the primary criteria by which 'primitiveness' in Simuliidae is judged (*i.e.* the wider the branching the more primitive a black fly is presumed to be).

Stone (1949) described a remarkable new genus, *Gymnopais*, whose larva lacked the typical feeding apparatus (labral fans) of black flies (compare figs. 30-31 with figs. 32-34 in chapter 3). A similarly modified but distinct genus, *Twinnia* Stone and Jamnback, 1955, was subsequently discovered in the mountains of eastern and western North America. Instead of filter-feeding in the typical simuliid fashion, larvae of *Gymnopais* and *Twinnia* browse upon epilithic algae or other food that is settled upon the substrate (Currie and Craig 1987). It was generally assumed that the fanless condition in black flies was primitive (based on the assumption of a close relationship between Simuliidae and Chironomidae), and that there must be a substantial phylogenetic gap between *Gymnopais* and *Twinnia* on the one hand, and *Prosimulium s.lat.* on the other (Rubtsov 1956, Grenier and Rageau 1960, Dumbleton 1963). Indeed, Rubtsov (1955) was so impressed with the fanless condition that he erected the subfamily Gymnopaidinae. Other workers were concerned about the manifest similarity of adults of *Twinnia* and *Prosimulium s.lat.*, and regarded these two forms as congeneric (Shewell 1958). However, most workers during the 1960's relegated *Gymnopais* and *Twinnia* to a separate subfamily or tribe.

In a classification that reflected notions about simuliid relationships during the 1960's Grenier and Rageau (1960) accepted a 3 subfamily system of Simuliidae: Parasimuliinae, Prosimuliinae, and Simuliinae. As in most previous classifications *Parasimulium* was segregated as a separate subfamily. Two tribes were recognized within Prosimuliinae: Gymnopaidiini (*Gymnopais* Stone and *Twinnia* Stone and Jamnback), and Prosimuliini (*Prosimulium* Roubaud). The subfamily Simuliinae included 3 tribes: Cnephiini (*Cnephia s.lat.* Enderlein), Austrosimuliini (*Gigantodax* Enderlein and *Austrosimulium* Tonnoir), and Simuliini (*Simulium s.lat.* Latereille). This was essentially the same system adopted by Dumbleton (1963), except that *Gigantodax* and *Cnephia s.lat.* were relegated to Prosimuliinae.

Although restricted in geographical scope Stone's (1965) classification of North American Simuliidae represented a considerable departure from other classifications proposed during the 1960's, particularly with respect to the taxonomic rank accorded certain primitive-grade taxa. Stone was not impressed enough with the features of *Parasimulium* to accord subfamilial status to members of that genus alone. Instead, he united the tribes Parasimuliini (*Parasimulium*), Prosimuliini (*Prosimulium s.lat.*), and Gymnopaidini (*Gymnopais,Twinnia*) in the single subfamily Prosîmuliinae. The genera *Cnephia s.lat.* and *Simulium s.lat.* constiuted the only other recognized subfamily, Simuliinae. No tribal-level segregates were recognized in this latter subfamily.

Most present-day notions about simuliid classification have been drawn from the efforts of two workers — I.A. Rubtsov and R. W. Crosskey. The former produced numerous works on the supraspecific classification of the family from 1937 (*et seq.*) to present. The most comprehensive account of Rubtsov's classification is embodied in his 1974 treatise about the evolution, phylogeny and classification of Simuliidae. There he recognized a total of 59 genera in four subfamilies as follows: Parasimuliinae (*Parasimulium*), Gymnopaidinae (*Twinnia, Gymnopias*), Prosimuliinae (*Prosimulium s.lat., Gigantodax, Procnephia, Paracnephia*), and Simuliinae (all other genera). A total of 5 tribes were recognized in Simuliinae: Austosimuliini, Cnephiini, Eusimuliini, Wilhelmiini, and Simuliini. This is the system followed by most Soviet and eastern European workers. Rubtsov is one of the few workers to have attempted to unravel the phylogenetic relationships of black flies, and to have incorporated this information in a classification. A summary of the hypothesized relationships is given in Figure 3.

In the classification followed by most western European and North American workers Crosskey (1981a, 1987) recognizes only 2 subfamilies of black flies, the Parasimuliinae (*Parasimulium*) and the Simuliinae (all other Simuliidae). The Simuliinae is divided into two tribes as follows: the Simuliini (*Austrosimulium* Tonnoir and *Simulium* Latreille) and the Prosimuliini (comprising all other simuliids). As opposed to the large number of genera recognized by Rubtsov, Crosskey (1987) adopted a rather conservative approach, recognizing only 23 genera. The intent of his classification was not necessarily to reflect the phylogenetic relationships of black flies, but rather to find some kind of "phyletic cleavage" between plesiotypic and more apotypic members.

2.3.2 Other taxonomic contributions:

A number of African forms are characterized by the lack of a pedisulcus, a weakly developed calcipala, absence of well-developed spiniform setae on the costa and other wing veins, an ill-formed pupal cocoon, and long terminal spines on the pupal abdomen. All of these character states, which are shared to some degree by members of *Parasimulium* and *Prosimulium s.lat.*, have been considered plesiotypic within Simuliidae. However, the wing venation of these African forms is evidently derived in lacking a definite fork in the radial sector. As a result of this combination of primitive and derived traits, the placement of these black flies has remained problematic. Most of the species were originally described in either *Prosimulium* Roubaud (de Meillon and Hardy 1951) or *Cnephia* Enderlein (*e.g.* Freeman and de Meillon 1953), and it was not until 1962 that a separate genus, *Paracnephia* Rubtsov, was recognized (Rubtsov 1962). Crosskey accepted this name as a subgenus of *Prosimulium s.lat.* and erected another subgenus, *Procnephia* Crosskey, for a small group of species that appeared to be intermediate in form between *Prosimulium s.str.* and *Paracnephia* (*e.g.* costa of female with hair-like macrotrichia only; male with some macrotrichia thickened, but not fully spiniform). The phylogenetic position of *Procnephia* and *Paracnephia* has remained uncertain to the present day. Crosskey (1981a) retained these taxa as subgenera of *Prosimulium s.lat.*, whereas Rubtsov (1974) regarded them as full genera within Prosimuliinae (fig. 3 b). In addition to the forms living in southern Africa, Rubtsov (*loc. cit.*) referred to *Paracnephia* the Australian species of "*Cnephia s.lat.*"

Davies (1965a, 1974) studied the monobasic genus *Crozetia*, whose larva possesses rudimentary, rake-like labral fans. Instead of filter feeding in the typical simuliid fashion, larvae use their fans to rake filamentous algae from the stones on which they live. Davies compared this arrangement with the fans of typical simuliids, together with the minute, bristle-like appendages that arise from the labra of first instar larvae of *Gymnopais*, *Twinnia*, and *Prosimulium s.lat.* He concluded that bristle-like labral appendages are primitive for Simuliidae (an example of 'ontogeny recapitulating phylogeny'), and that evolution has proceeded in two directions: (1) to complete loss in *Gymnopais* and *Twinnia*, whose ancestors never before possessed fans; and (2) to elaboration of the bristles into a raking device, such as found in larvae of *Crozetia*. Davies assumed that this latter type of fan gave rise to the elegant filtering devices of typical simuliid larvae. Although no attempt was made at a reclassification of the family, it is implicit that *Gymnopais* and *Twinnia* would have to be considered the sister group of all other simuliids.

Wood (1978) has taken the exact opposite view. He argued that fans are not only a fundamental (and homologous) feature of Simuliidae, but of related families as well (Tanyderidae, Ptychopteridae, Culicidae, Dixidae). Thus, absence of fully developed fans in larval Simuliidae (and by extension in larvae of other families of Culicomorpha *viz.* Chaoboridae, Thaumaleidae, Chironomidae, Ceratopogonidae) must be the result of loss. This will be discussed in greater detail in the section 'Monophyly, sister-group relationship, and groundplan of Simuliidae'.

Wygodzinsky and Coscarón (1973) surveyed the primitive-grade simuliids (Prosimuliini *sensu* Crosskey) of the Neotropical region, and proposed a number of sister-group relationships based on that fauna. Although they did not concern themselves directly with the higher classification of the family, Wygodzinsky and Coscarón asserted that most definitions of Prosimuliini were based on symplesiotypic characters, and could not be maintained in a cladistic system. This was the first attempt to view simuliid relationships in a cladistic sense.

Special mention is required about the role of cytology in resolving simuliid relationships. Studies of the larval salivary gland chromosomes have shown that differences in banding patterns can be used to reveal biologically distinct sibling species in isomorphic larvae. Further, the pattern of chromosomal inversions (the breaking points at which can occur at any of several thousand sites) can be analysed in a sequential fashion to generate a "cytophylogeny", the rationale being that the probability of the same inversion occuring independently more than once is remote. The cytophylogeny is unrooted because the point of origin, the so-called "standard sequence", is chosen on the basis of its "centrality", and not on the basis of out-group comparison. In other words, for any given arm of the chromosome the standard sequence occurs in a number of related taxa, and gives rise to the largest number of individual derivatives. Thus, while Rothfels and Freeman (1966) have shown that *Prosimulium* <-> *Helodon* <-> *Twinnia* <-> *Gymnopais*, the direction of evolution cannot be determined (*i.e.* it is unclear whether *Frosimulium* or *Gymnopais* is the most primitive member of the sequence).

At present, fewer than 10% of the world total of nominal species have been studied chromosomally (Crosskey 1987). As the world simuliid fauna becomes better known, it may be possible join together the many small cytophylogenies into a comprehensive system of hypothesized relationships. However, it will remain to the morphotaxonomist to determine the direction of evolution, by using external structural information to root the system of relationships suggested by cytology. This one weakness not withstanding, cytotaxonomy will continue to be an important component of phylogenetic investigation, because it provides an independant means by which morphologically derived hypotheses can be tested.

2.4 Simuliid fossil record

The paleontological record adds little to our knowledge about simuliid relationships as few fossil black flies are known. The best known inclusions are from Baltic amber of Oligocene age, although the species, *Simulium oligocenicum* Rubtsov, is referable to a modern group (Rubtsov 1936). Craig (1977) has clearly shown that *Pseudosimulium humidum* Westwood, a fossil described from Jurassic rocks, is not a simuliid, but is rather more likely to be a ceratopogonid. The fossil genus *Simulidium* Westwood, 1854, also from Jurassic rocks, has been referred to the Bibionomorpha (Rohdendorf 1974). More recently Hong (1982) proposed the new genus *Liauningius* for a purported simuliid fossil from Jiuquan Basin, China. The genus was erected for a Jurassic fossil originally described as *Chironomaptera robustus* Lin, 1986 (Diptera: Protendipedidae Rohdendorf, 1962). Although I have not examined this material first hand, it seems clear from the original description (and indeed from Hong's own illustrations; *cf.* pg. 169, figs. 146 - 147) that *Liauningius* is a non-simuliid. Apart from the fact that the fossil bears little superficial resemblance to any simuliid that I am aware of, it possesses no wings and has a 13 articled antennal flagellum!

The oldest fossils definitely attributed to Simuliidae are from the lower Cretaceous Koonwarra fossil bed, South Gippsland, Australia (Jell and Duncan 1986). The material, which is preserved in fine clay laminae, consists of a single complete adult, a dissociated wing, and 14 larvae. The adult is not a simuliid, and is possibly an empidid. I have not examined the dissociated wing, but it would seem from the photograph (*cf.* Jell and Duncan 1986, fig. 49 F) that it is also non-simuliid. The larvae are unquestionably simuliid, but are preserved in such a way that diagnostic features at the generic level are not clearly manifest. However, it appears that the larvae lack apotypic characters that would permit placement in either Parasimuliinae or Prosimuliini, and instead possess features that suggest relationship with the Australian "*Cnephia*" of authors (*nec Cnephia* Enderlein) (Craig and Currie, in prep.). The Koonwarra fossils are therefore referred to the tribe Simuliini, as defined in the present work.

2.5 Materials and methods

2.5.1 Materials

Taxa examined for structural features of Simuliidae included representatives of 34 of the 75 genus-group segregates listed as valid by Crosskey (1987) [see Appendix I]. Of the 41 taxa not examined, 35 are recognized as subgenera of *Simulium s.lat.* These latter belong to a relatively derived clade of simuliids, and so knowledge about their character states is not essential for this investigation of the primary evolutionary lineages. Structural features of the other six taxa (*Astoneomyia* Peterson, *Araucnephioides* Wygodzinsky and Coscarón, *Cnesiamima* Wygodzinsky and Coscarón, *Lutzsimulium* d'Andtretta and d'Andtretta, *Novaustrosimulium* Dumbleton, and *Sulcicnephia* Rubtsov) were determined as far as possible from descriptions and illustrations in the literature.

The majority of material examined is from my own collection, and from specimens housed in the Department of Entomology, University of Alberta. Character-state distributions in *Mayacnephia* Wygodzinsky and Coscarón, *Cnesia* Enderlein, *Gigantodax* Enderlein, *Araucnephia* Wygodzinsky and Coscarón, *Tlalocomyia* Wygodzinsky and Díaz Nájera, and in the Australian species described in the genus *Cnephia* Enderlein (but undoubtedly belonging elsewhere), are based, in part, on specimens in the Canadian National Collection, Ottawa. Character-state distributions in *Procnephia* Crosskey, *Paracnephia* Rubtsov, and *Urosimulium* Contini are based, in part, on specimens in the British Museum (Natural History), London. Specimens of *Levitinia freidbergi* Beaucournu-Saguez and Braverman were made available for study by Mme. Beaucournu-Saguez, Laboratory of Applied Parasitology and Zoology, Faculty of Medicine, Rennes, France. The lower Cretaceous fossil material, from the Koonwarra fossil bed, South

Gippsland, Victoria, was obtained on a loan from the Palaeontological Collection, Museum of Victoria, Melbourne.

2.5.2 Specimen preparation and illustration

Ethanol-preserved specimens were used for most of the illustrations. Larger preparations, such as whole mounts, were oriented in a small blob of petroleum jelly, which in turn was situated on the bottom of a welled slide. The well was then flooded with glycerin and covered with a cover glass. Smaller preparations, such as dissections, were either mounted in Euparol, or were cleared and mounted in polyvinyl lactophenol. Most line drawings were prepared with the aid of a camera lucida mounted on a Wild M5 stereomicroscope. Drawings of smaller structures were executed with the aid of a drawing tube mounted on a Leitz Wetzlar SM-LUX light microscope. Photomicrographs of slide mounts were taken with a Wild photoautomat camera mounted on a Wild M20 compound microscope.

Specimens used for scanning electron microscopy (SEM) were dehydrated through 98% ethanol and critical-point dried. Dried specimens were mounted on SEM stubs to which double-sided sticky tape was applied. The material was gold coated with a sputter coater and photographed with a Cambridge Stereoscan 250 scanning electron microscope.

Cladograms and diagrammatic representations of character transformations were executed with the aid of a software program designed for a Macintosh™ microcomputer.

2.5.3 Classification

The higher classification of Simuliidae is not universally agreed upon, with a number of schemes having been proposed over the last quarter of a century. For the purposes of the present study I have followed a two-subfamily-arrangement for black flies, in which Parasimuliinae comprises *Parasimulium s.lat.*, and Simuliinae comprises all other genera. In this respect, the system is similar to the classifications accepted by most western specialists. Where it departs is in recognition of tribes within Simuliinae; *viz.* Prosimuliini and Simuliini. Crosskey, for example, interprets Prosimuliini in a sense that includes 21 of the 23 genera recognized in Simuliinae. I have defined Prosimuliini in a rather narrower sense, comprising only the following genus-group taxa: *Twinnia, Gymnopais, Levitinia* and *Prosimulium s.lat.* (*Distosimulium, Helodon, Parahelodon, Prosim*[illegible] *s.str.*, *Urosimulium*[1]). I refer all other genera of Simuliinae, including *Procnephia* and *Paracnephia*[2], to the tribe Simuliini. The rationale for the system adopted in the present work is given later in this chapter. A summary of some recent classifications of Simuliidae is given in Table 2.1.

It is not within the context of the present chapter to consider the validity (or ultimate rank) of genus-group segregates. Consequently, I have endeavored to use a system that is already familiar to most students of Simuliidae. Except for the differences outlined above, I have followed essentially the system of genera and subgenera recognized by Crosskey (1981, 1987). A major advantage of this system is that comparatively few genera are recognized (22), reflecting the structural homogeneity of Simuliidae relative to other

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[1] Crosskey (1987) relegates members of *Urosimulium* to the "*Prosimulium s.str. aculeatum* group".

[2] Crosskey (1987) treats *Procnephia* and *Paracnephia* as subgenera of *Prosimulium s.lat.*

Table 2.1. Comparison of some recent classifications of Simuliidae.[1]

Crosskey (1987)

- Subfamily **PARASIMULIINAE**
  - *Parasimulium s.lat.* Malloch
- Subfamily **SIMULIINAE**
  - Tribe PROSIMULIINI
    - *Araucnephia* Wygodzinsky & Coscarón
    - *Araucnephioides* Wygodzinsky & Coscarón
    - *Cnephia* Enderlein
    - *Cnesia* Enderlein
    - *Cnesiamima* Wygodzinsky & Coscarón
    - *Crozetia* Davies
    - *Ectemnia* Enderlein
    - *Gigantodax* Enderlein
    - *Greniera* Doby & David
    - *Gymnopais* Stone
    - *Levitinia* Chubareva & Petrova
    - *Lutzsimulium* d'Andretta & d'Andretta
    - *Mayacnephia* Wygodzinsky & Coscarón
    - *Metacnephia* Crosskey
    - *Paraustrosimulium* Wygodzinsky & Coscarón
    - *Prosimulium s.lat.* Roubaud (including *Procnephia* Crosskey and *Paracnephia* Rubtzov)
    - *Stegopterna* Enderlein
    - *Sulcicnephia* Rubtzov
    - *Tlalocomyia* Wygodzinsky and Díaz Nájera
    - *Twinnia* Stone & Jamnback
  - Tribe SIMULIINI
    - *Austrosimulium s.lat.* Tonnoir
    - *Simulium s.lat.* Latreille

Rubtzov (1974)[2]

- Subfamily **PARASIMULIINAE**
  - *Parasimulium s.lat.* Malloch
- Subfamily **GYMNOPAIDINAE**
  - *Gymnopais* Stone
  - *Twinnia* Stone & Jamnback
- Subfamily **PROSIMULIINAE**
  - *Gigantodax* Enderlein
  - *Prosimulium s.lat.* Roubaud (including *Procnephia* Crosskey and *Paracnephia* Rubtzov)
- Subfamily **SIMULIINAE**
  - Tribe AUSTROSIMULIINI
    - *Austrosimulium s.lat.* Tonnoir
  - Tribe CNEPHIINI[3]
    - *Cnephia* Enderlein
    - *Greniera* Doby & David
    - *Ectemnia* Enderlein
    - *Lutzsimulium* d'Andretta & d'Andretta
    - *Metacnephia* Crosskey
    - *Simulium s.lat.* Latreille (in part)
    - *Stegopterna* Enderlein
    - *Sulcicnephia* Rubtzov
  - Tribe EUSIMULIINI[4]
    - *Simulium s.lat.* Latreille (in part)
  - Tribe SIMULIINI
    - *Simulium s.lat.* Latreille (in part)
  - Tribe WILHELMIINI
    - *Simulium s.lat.* Latreille (in part)

Classification based on cladistic relationships, as discussed in text.

- Subfamily **PARASIMULIINAE**
  - *Parasimulium s.lat.* Malloch
- Subfamily **SIMULIINAE**
  - Tribe PROSIMULIINI
    - *Gymnopais* Stone
    - *Levitinia* Chubareva & Petrova
    - *Prosimulium s.lat.* Roubaud (excluding *Procnephia* Crosskey and *Paracnephia* Rubtzov)
    - *Twinnia* Stone & Jamnback
  - Tribe SIMULIINI
    - *Araucnephia* Wygodzinsky & Coscarón
    - *Araucnephioides* Wygodzinsky & Coscarón
    - *Austrosimulium* Tonnoir
    - *Cnephia* Enderlein
    - *Cnesia* Enderlein
    - *Cnesiamima* Wygodzinsky & Coscarón
    - *Crozetia* Davies
    - *Ectemnia* Enderlein
    - *Gigantodax* Enderlein
    - *Greniera* Doby & David
    - *Lutzsimulium* d'Andretta & d'Andretta
    - *Mayacnephia* Wygodzinsky & Coscarón
    - *Metacnephia* Crosskey
    - *Paracnephia* Rubtzov[5]
    - *Paraustrosimulium* Wygodzinsky & Coscarón
    - *Procnephia* Crosskey[5]
    - *Simulium s.lat.* Latreille
    - *Stegopterna* Enderlein
    - *Sulcicnephia* Rubtzov
    - *Tlalocomyia* Wygodzinsky & Díaz Nájera

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[1] For comparative purposes, the generic concepts used in this table are mainly those of Crosskey (1987)

[2] Rubtzov (1974) did not take into consideration several of the Neotropical genera treated by Wygodsinsky and Coscarón (1973)

[3] The family-group name Stegopternini Enderlein has priority over Cnephiini Grenier & Rageau when *Stegopterna* and *Greniera* are contribal (Crosskey 1985).

[4] Nevermanniini Enderlein is the oldest available family-group name for the genera included in this tribe (Crosskey 1985).

[5] This taxon is best ranked as a full genus when referred to Simuliini.

Culicomorpha. It is also less cumbersome than the system favoured by most Soviet and eastern European workers (*e.g.* Rubtsov 1974), in which numerous genera are recognized (59+). A disadvantage of Crosskey's scheme, although not restricted to his alone, is that certain generic concepts are formed solely on the basis of phenetic divergence or similarity of constituent species. Thus, relatively aberrant groups of species, such as those belonging to the segregates *Twinnia* and *Gymnopais,* are accorded full generic rank, despite the fact they are derived from a *Prosimulium s.lat.* ancestor (Wood 1978). In a strictly cladistic classification, such taxa could only be ranked at the level of subgenus. However, this does not present a serious problem in the context of the present chapter.

The relationships of some black flies are so inadequately known that their generic placement remains uncertain. One such group is the Australian species included in *Cnephia* Enderlein. This is a group of species whose members are only distantly related to *Cnephia s.str.* Although Rubtsov (1974) relegates these species to *Paracnephia*, there is insufficient evidence at present to include them in that genus. For the present, I refer to these species as the Australian "*Cnephia*".

2.5.4 Structural characters and terms for structures

In this chapter I follow the general structural terms for Diptera as outlined by Teskey (1981). For structures that are unique (autapotypic) for Simuliidae I follow largely the terms of Peterson (1981). Exceptions to this scheme have already been published (Currie 1986), and will not be considered in detail here.

One of the exceptions given by Currie (*loc. cit.*) is the use of the term "gill". In Simuliidae, as in certain other families of aquatic Diptera, the paired dorsolateral appendages of the pupal thorax bear a plastron network. In such instances the term spiracular gill may be applied appropriately. However, as the pupal respiratory appendages of several culicomorph families lack a plastron network, I have adopted the term "respiratory organ" to provide an appropriate common term.

For specific structures of the larval head I use the terms of the following: Craig (1974) for the labrum; Craig and Borkent (1980) for the maxillary palpus, and Craig and Batz (1982) for the antenna. For sclerotized features of larval abdominal segment nine, I have used largely the terms of Barr (1984).

2.5.5 Phylogenetic methods

Relationships among primary lineages of Simuliidae were determined using phylogenetic principles *sensu* Hennig (1966). Several excellent treatments of the "cladistic method" have been produced in recent years (*e.g.* Eldredge and Cracraft 1980, Wiley 1981), and so only a brief account will be given here.

By lineage I mean one or more taxa that share a common history not shared by other taxa. Such lineages are defined by shared, derived homologous characters termed synapotypies[3]. Hypotheses of relationship based on shared primitive character states (symplesiotypies), or by independently derived non-homologous character states, such as convergences or parallelisms (homoplasies), are rejected. Among the primary goals of the phylogenetic systematist are: (1) to distinguish between synapotypic and plesiotypic character states, and (2) to recognize homoplasy.

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[3] The suffix "typy" is used in favor of the more commonly used "morphy" because both structural and non-structural characters (*e.g.* behavioural, ecological) can be used to define lineages (Tuomikoski 1967).

The evolutionary polarity of characters (*i.e.* the direction of character-state evolution) can be assessed in a number of different ways (see reviews by Crisci and Stuessy 1980, de Jong 1980, and Stevens 1980). For most characters, I determined character-state polarity using the out-group comparison method, a technique summarized by Watrous and Wheeler (1981) as follows: for a given character with two or more states within a group, the state occurring in related groups is assumed to be primitive. Relationships of Simuliidae to other Diptera are reasonably well established, and are considered in detail elsewhere in this chapter.

Some character states, such as transformations of simuliid autapotypies (*i.e.* transfomations of character states occurring within Simuliidae but in no other family), cannot be polarized using the out-group method — at least not very convincingly. For such characters, an in-group method of polarization was used. For some structures character states were judged to be primitive if they were widely and commonly distributed throughout the family. The shortcomings and pitfalls of this technique were clearly documented by Watrous and Wheeler (1981) and are not repeated here. However, in recognizing the limitations of the technique, interpretations based solely on "commonality" were kept to a minimum. But while it is understood that in-group analysis, in itself, is not a reliable indicator of character state polarity, hypotheses about synapotypy versus sympleisiotypy can be based on congruence or non-congruence of character-state transformations, as judged from other characters.

Hypotheses of synapotypy relative to homoplasy are normally dependent on parsimony arguments as there is seldom decisive morphological or ontogenetic evidence forwarded to indicate that two similar character states are nonhomologous (Wiley 1981). Ideally, relationships are established using characters most reliable as phylogenetic indicators. States of characters that are deemed less reliable as phylogenetic indicators, and that are in conflict with hypotheses based on primary characters, are judged to be homoplastic. In the present work the relative value of a presumed synapotypy is judged by the criteria developed by Hecht & Edwards (1976). Five levels of reliability are recognized as follows, proceeding from most reliable to least reliable: (1) apotypic states that are both innovative and unique, (2) those that are part of a functional complex, (3) those whose development is related to ontogenetic or allometric processes, (4) those that are the result of reductions, and (5) those that are the result of loss.

Although I have accepted the general criteria of Hecht and Edwards (*loc. cit.*) I have not adopted a comprehensive weighting scheme that distinguishes among all categories. Instead, I recognize only two general categories of synapotypy based on the overall reliability of a character state as a phylogenetic indicator. The criteria for each category are:

(1) *Primary synapotypy.* — For a character state to be so designated it must (a) fall within one of the first two categories as outlined by Hecht and Edwards (*i.e.* the character state must be both innovative and unique within Simuliidae and (b) not be homoplastic within Culicomorpha. Both (a) and (b) must be satisfied for a character state to be considered a primary phylogenetic indicator.

(2) *Secondary synapotypy.* — A character state is designated thus if it (a) is subject to influence by ontogenetic or allometric processes; (b) is the result of reduction or loss; (c) is homoplastic within Simuliidae; or (d) has been so little investigated in Simuliidae that conclusions about (c) cannot be made. If a character state is characterized by any of the criteria given above, it is regarded as a secondary phylogenetic indicator.

The basic topology of the cladogram is generated from primary synapotypies. Secondary syapotypies are added to the cladogram in view of the relationships suggested by primary characters. A similar two-level analysis was developed by Anderson (1987).

2.6 Structural and ecological features of the immature stages of *Parasimulium crosskeyi* Peterson

2.6.1 Introduction

Descriptions of the first- and second-instar larvae of *Parasimulium stonei*, and of the larva and pupa of *P. crosskeyi*, are provided by Borkent and Wood (1986) and Courtney (1986). However, in view of recently collected additional material, a redescription of the immature stages of *P. crosskeyi* is in order because I have reinterpreted several of the characters discussed in the original work, and a number of phylogenetically important features have subsequently come to light. A firm understanding of such features is paramount for establishing relationships among the primary clades of Simuliidae.

The following description is based on 43 larvae (middle- to late-instar) and 6 pupae, all collected from 26 - 27 June, 1986, Wahkeena Creek, Multnomah Co., Oregon (45° 34'N, 122° 07'W). All material was collected from within seeps adjacent to the main stream, and not from the main stream *per se*. Numerous adults were also collected as they hovered or rested beneath the streamside vegetation; but as males and females have already been adequately described, it is not necessary to consider them any further here [see Peterson (1977) and Wood and Borkent (1982) for descriptions of adults of *P. crosskeyi*].

A single, middle instar larvae of *Parasimulium* was collected on 28 June, 1986, from a seep adjacent to Trail Creek, Lane Co., Oregon (44° 00'N 122° 10'W). The larva was agreeable in all respects to similarly-sized *P. crosskeyi* from Wahkeena Creek; however, only adults of *P. stonei* were represented at the Trail Creek site. As middle- and later-instar larvae of *P. stonei* have yet to be described, it is uncertain as to which species the larva belongs. The hypostoma of second-instar *P. stonei* appears to be readily distinguishable from those of middle- and later-instar *P. crosskeyi* — at least as inferred from the illustrations provided in the original descriptions [*cf.* Borkent and Wood (1986, fig. 3e) and Courtney (1986, fig. 5)]. If the Trail Creek larva belongs to *P. stonei*, as suggested by its association with adults of that species, then either the hypostoma undergoes marked structural changes after the second instar, or the only known second-instar larva is aberrant. The alternative, that the larva in fact belongs to *P. crosskeyi*, cannot be rejected solely on the basis of its lack of association with conspecific adults. It is clear that additional discoveries will have to be made to determine the true identity of later-instar *P. stonei* larvae. Adults of *P. stonei* have been well described by Peterson (1977) and Peterson and Courtney (1985).

2.6.2 Description

Larva (penultimate instar). Length ca. 5 mm. Body translucent in live specimens, white in specimens preserved in alcohol or Carnoy's solution (1 part glacial acetic acid : 3 parts 98% ethanol); alimentary canal readily visible through integument, as darkened, mediolongitudinal stripe. Head capsule (fig. 7) generally pale yellow except darkly sclerotized portions of mouthparts, with many fine, small, irregularly situated setae; cephalic apotome without pigmented spots at points of muscle insertion; ecdysial line barely distinguishable; stemmata unpigmented, rarely with narrow, longitudinal, pigmented band ("eyebrow") dorsally. Antenna (fig. 7) distinctly shorter than labral-fan base, extended 3/4 distance to apex; membranous antennal base (fig. 25, mab) broad basally, tapered distally, apical portion elongate, subrectangular, somewhat flattened dorsoventrally; bacteria-covered multiporous sensillum (bms) basolaterally on membranous antennal base (bacteria absent from some specimens) (fig. 25); flagellum not annulated, of single, slender article (distal article *sensu* Currie 1986), concolorous with labral-fan base, with fine hyaline reticulations, basally with pair of multiporous peg sensilla, apically with single uniporous cone sensillum. Labral fan fully developed, golden brown; base with moderately dense series of fine setae dorsally; primary fan of 17 - 20 slender, delicate, fringed rays (fig. 26); secondary fan triangular, flattened, of 16 - 19 rays, their tips in straight line parallel to labral-fan stalk. Mandible (fig. 27) with inner, subapical ridge with about 18 - 21 small to moderately large serrations (ms); mandibular phragma darkly sclerotized, separated from posterolateral margin of hypostoma by wide gap. Maxillary palpus (fig. 30) 2.5 - 3 times as long as width at base; spicules absent; sensilla in circular configuration at apex. Hypostoma (fig. 28) with 1 large and 5 small setae per side; teeth arranged in 3 distinct groups: central group consisting of a long median tooth, longer than width at base, and 3 or 4 irregularly positioned submedian teeth (in most specimens with 2 submedian teeth on one side, and 1 on other; rarely with 3 on one side, and 1 on other); lateral group (on either side of central group) more prominent than central group, separated from latter by deep slot, lateral tooth longest, medial margin with 2 sublateral teeth, lateral margin with 2 small paralateral teeth (not evident on some specimens); margins of median, outermost sublateral, and lateral teeth with minute serrations; lateral margin of hypostoma with 3 - 8 lateral serrations per side. Hypostomal bridge (fig. 7) much longer than hypostoma. Postgenal cleft absent (fig. 7). Postocciput (fig. 7) narrow, nearly complete dorsally, median gap between dorsal arms narrow; cervical sclerites transverse, completely enclosed by dorsal arms. Suboesophageal ganglion white, visible through cuticle of head capsule. Prothoracic proleg (fig. 29) elongate, its apex extended to level of (or anterior to) hypostomal groove; lateral plate of proleg absent. Abdomen with segments 1 - 4 rather narrow, segment 5 moderately and uniformly expanded, segments 6 -8 tapered posteriorly; segment 8 ventrally with large, inflated, conical, posteroventrally directed lobe (mvt), greater than 1/3 depth of abdomen at point of attachment (fig. 48); rectal setulae present (fig. 32); anal papillae of 3 simple digitate lobes. Anal sclerite (fig. 31) with dorsomedian sclerite (dms) crescent shaped; dorsal arms (da) relatively broad, flattened, somewhat raised laterally, terminates as a hemispherical or subrectangular plate (terminal plate, tp); ventral arms (va) not connected with dorsomedian sclerite, their proximal extremities midlaterally on abdominal segment 8, their apices nearly in contact ventromedially; spindle-shaped sclerite ventromedially (ventromedian sclerite, vms), immediately anterior to gap formed between apices of ventral arms. Posterior proleg (figs. 31, 32) of 12 -16 hooks in 140 - 160 rows.

Pupa. Length 2.0 - 3.5 mm. Integument generally slightly sclerotized, nearly transparent, with yellowish cast. Respiratory organ (fig. 8) nearly equal in length to pupal body; base cylindrical, elongate, unpigmented, lacking plastron network (fig. 33); hole in base of respiratory organ ("basal fenestra", bs) small, ventral (figs. 33, 34); felt chamber (fc) present as an internal continuation of tracheal trunk (figs. 8, 33, 34), closely associated with dorsal wall of respiratory-organ base, terminated near origin of respiratory trunks; respiratory-organ base branched into two main trunks; dorsal trunk simple; ventral trunk short, divided horizontally into 2 filaments of about equal length; total number of respiratory filaments 3; filaments rather inflated, shallowly annulated, opaque, with a plastron network (fig. 35). Head with numerous, minute, raised granules; antenna of male and female extended beyond hind margin of head by one or two segments. Thorax (fig. 36) with numerous, minute, raised, peg-like granules; trichomes slender, 8 per side. Abdominal segment 3 with tergite and sternite fused in form of a ring; segments 4 - 8 with tergites and sternites separated by broad area of striated pleural membrane; latter without distinct sclerotized plates (pleurites) or recurved hooks (fig. 17). Tergites (fig. 37) without row of short, fine, posteriorly directed spines (spine combs) near anterior margin; tergites 5 -9 with, at most, 8 tiny setae along posterior margin. Terminal hooks (fig. 38, th) relatively short, their bases rather swollen; spines nearly vertical or with a slight anterior inclination, their tips, at most, only slightly divergent; each with a moderately long, slender seta on swollen base anteriorly. Sternites (fig. 39) 5 - 7 each with one pair of large, anteriorly directed hooks (rh); hooks borne on posteroventrally directed tubercles; sternites 6 - 7 complete, not divided medially by area of longitudinally striate membrane. Cocoon a thin to moderately thick, loosely woven sleeve with adherent debris, both organic and inorganic; cocoon enclosing all of pupa except respiratory organ.

2.6.3 Natural History

Larvae, pupae, and teneral adults of *Parasimulium crosskeyi* have been reported from the "hyporheic area"[4] of Wahkeena Creek, Oregon (Courtney 1986). However, several lines of evidence suggest a hypogean or phreatic[5] origin for this material: (1) *Parasimulium* was collected from a seep adjacent to Wahkenna Creek (personal observation; Courtney *loc. cit.*), and not from the main stream *per se*; (2) *Parasimulium* were collected in association with typical inhabitants of the hypogean zone, such as isopods and amphipods (E. L. Bousfield, personal communication); (3) neither *Parasimulium* nor any of the known hypogean elements of the seep have been collected from Wahkeena Creek, despite intensive surface and subsurface sampling (personal observation, Wood and Borkent 1982); (4) the immature stages of *Parasimulium* have some structural adaptations typical of cavernicolous organisms (blind, unpigmented larva; unpigmented pupa); (5) adults of *Parasimulium* were commonly observed only within a 100 m distance of the seep (personal observation; see also Wood and Borkent 1982, fig. 1). If *Parasimulium* were distributed throughout the hyporheos of Wahkeena Creek, adults would be expected over a much wider area.

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[4] Hyporheic refers to the interstitial environment that is formed in the mixture of sand, gravel, and rocks beneath streams (Williams 1984).

[5] Hypogean or phreatic refers to underground aquatic habitats such as subterranean springs.

All material collected in the present study was taken from seeps that issued at least 10 cm above the Wahkeena Creek water line. Stones were carefully remove from the mouth of the seep and examined for *Parasimulium*. This process was continued for a distance of up to 1 m into the bank, or until a point where no further specimens were found. A number of seeps were examined in this fashion, and a recurring pattern became evident. Each seep was overlain by a densely rooted layer of humus, which precluded emergence of adults from anywhere but the mouth. The subterranean flow was definitely channelized, with the main channel consisting of poorly sorted stones and cobbles. The area surrounding this passageway consisted of a wider range of particle sizes, and was held together by a matrix of interstitial sand and clay. As a result of this arrangement, water passed much more copiously through the channel than it did the surrounding area. Water velocity estimates for the channel ranged from 20 - 40 cm/sec.

Mature larvae and pupae (up to penultimate instar) were encountered only within the first 20 cm of the mouth of the seep. Earlier instars were predominantly distributed 30 - 60 cm into the seep. Most larvae were encountered in groups of 2 - 5, side by side with their posterior ends oriented into the current. Such banding patterns are typical of filter-feeding simuliids, and strongly suggest that *Parasimulium* larvae were feeding in this fashion. This does not suggest that *Parasimulium* larvae are unable to engage in any one of several other feeding strategies adopted by larval black flies (*e.g.* browsing, deposit feeding, predation), but it would seem from the structure of the mouthparts (labral fan, mandible, hypostoma) that filter-feeding is the primary means by which food is procured. If this is so, then the feeding mechanism of *Parasimulium* can also be taken against the hypothesis of a hyporheic habitat, for it is doubtful there is sufficient current in the hyporheos of Wahkeena Creek to facilitate filter feeding. Williams and Hynes (1974) showed a substantial decrease in current velocity between the surface flow of a stream, and that found at 10 cm below the stream bed. The velocity contined to decrease to a depth of 40 cm (0.04 cm/sec), after which no flow could be detected with the apparatus used.

Despite the fact that nearly 150 larvae of *Parasimulium crosskeyi* have been field-collected there has yet to be found a single last-instar larva (personal observation; D. A. Craig and G. W. Courtney, personal communication). Moreover, pupae seem to be far less represented in the seep than would be expected given the relative frequency of larvae and adults. In other black flies, the pupal exuviae typically remain attached to the substrate for a considerable period following emergence. This, plus the fact that mature larvae are primarily distributed near the mouth of the seep, suggests that last-instars may be leaving the seep to pupate. Unfortunately, I was unable to find *Parasimulium* beyond the mouth of the seep, and so the location of the pharate pupa remains uncertain. The Wahkeena Creek site was not ideal for this part of the investigation because the seeps extended only for a short distance (< 0.5 m) before terminating in a flooded ditch (see Courtney 1986 for a fuller description of the site).

The hypothesis of an extra-hypogean pupation site seems plausible considering the potential problems of subterranean emergence. It would seem unlikely that a newly emerged adult could work its way through the labyrinth if it had pupated deep within the spring. But even if an adult were able to crawl above the waterline, it seems unlikely that it would be able to work its way through the dense humus ceiling overlaying the spring.

Discovery of the last-instar larva would be of interest not only in the context of the present study, but also for the cytological information it might yield. Last-instar simuliid larvae possess polytene chromosomes large enough to permit resolution of their banding patterns. Such chromosomal information can be used to construct transformations ("cytophylogenies"), which in turn can be used to test phylogenies based on other characters. None of the material collected to date has proven suitable for chromosomal analysis (P. H. Adler, personal communication).

A few females of *Parasimulium* hovered above the mouth of the seep, but were not seen to enter. They probably have a similar behaviour to ovipositing females of *Twinnia*, which fly upstream until they find the source of the spring (Wood 1978). It would be of interest to determine how the eggs are deposited, and how the early-instar larvae come to be situated so deep in the substrate. D. M. Wood (personal communication) found that females of *P. crosskeyi* could crawl about in water placed in the bottom of a vial, and so it seems possible that they could enter the mouth of the spring to oviposit.

2.7 Monophyly, Sister-group relationship, and groundplan of Simuliidae

Because of the structural homogeneity of Simuliidae, and the distinctiveness of its members from other Nematocera, the monophyly of the family has not been questioned seriously. Below I enumerate 23 characters that may be considered groundplan apotypies of the family. But before a meaningful discussion of characters can be undertaken, it is first necessary to consider relationships of Simuliidae with cladistically related families.

For the present study I have adopted essentially the concept of the infraorder Culicomorpha as outlined by Hennig (1973, 1981). Under this scheme, Culicomorpha is a well-defined monophyletic lineage comprising two sister groups; the superfamily Culicoidea (Dixidae, Culicidae, Chaoboridae), and the superfamily Chironomoidea (Thaumaleidae, Simuliidae, Ceratopogonidae, Chironomidae) (fig. 1). Synapotypic characters for Culicomorpha and its consituent superfamilies have been indicated elsewhere (Hennig *loc. cit.,* Wood 1978) and will not be considered in detail here. However, it is expedient to consider some recent additional evidence that bears on relationships among Culicomorpha.

Wood (1978) has argued convincingly that some form of labral feeding brush is present in the larva of not only Dixidae, Culicidae, and Simuliidae, but of Ptychopteridae as well. Thus, instead of the Ptychopteridae belonging to the Psychodomorpha, as held by Hennig (1973), the family is best considered the sister group of Culicomorpha (D. M. Wood, personal communication). Indeed, in the classification given in the Manual of Nearctic Diptera (McAlpine *et al.* 1981), the superfamily Ptychopteroidea (comprising Ptychopteridae) is recognized in support of this hypothesized relationship. This is the interpretation followed in the present work. The labral fan has evidently been lost independently in larvae of Chaoboridae, Thaumaleidae, Ceratopogonidae, and Chironomidae.

The Hennigian concept of Culicomorpha has received almost universal acceptance among dipterists, with perhaps the only contentious issue being the placement of Thaumaleidae. Rohdendorf (1974), for example, placed Thaumaleidae and Perissommatidae together as the sister group of all other "Tipulimorpha" (= Tipulomorpha + Psychodomorpha + Culicomorpha of Hennig). G. C. D. Griffiths (personal communication) has drawn my attention to the work of Whitten (1960), which shows that larvae of Dixidae, Culicidae, Thaumaleidae (as Orphnephilidae), Simuliidae, Ceratopogonidae, and Chironomidae all lack the three ventral anastomoses normally present in the tracheal system of larval Diptera. This provides further support for the monophyly of Culicomorpha, and reinforces the inclusion of Thaumaleidae in that infraorder.

Having considered the relationships of Culicomorpha in general, it is now possible to consider relationships within the superfamily Chironomoidea. Hennig (1973, 1981) provided the following characters in support of the monophyly of this taxon: (1) 1st anal vein (A_1) not extended to hind margin of wing, terminated very close to cubitus; (2) costa not extended far beyond terminus of R_1; (3) first branch of radial sector (either R_{2+3} or R_2) terminated in radius (R_1); and (4) presence of prothoracic and posterior prolegs in the larva. Another character that may also be synapotypic of Chironomoidea is the presence on the pupal respiratory organ of a plastron network. The plastron is a respiratory adaptation of aquatic insects whose habitat is subject to frequent and extensive fluctuations in water level (Hinton 1968). Presence of such a structure is well established on the pupal respiratory organs of Simuliidae and plesiotypic Chironomidae (Aphroteniinae, Podonominae, Tanypodinae, and Telmatogetoninae [?] — *cf.* Coffman 1979), but I have also found this to be true for *Thaumalea americana* Bezzi. It therefore seems possible that a plastron is part of the groundplan of Chironomoidea. A plastron has yet to be documented on the pupal respiratory organ of Ceratopogonidae, although it is unclear as to whether this represents absence or lack of study.

Of the four families that comprise Chironomoidea, Thaumaleidae is considered to be the most primitive. This is based, in part, on the plesiotypic retention of spiracles (amphipneustic condition) in larvae of Thaumaleidae, but their absence (apneustic condition) from larvae of most other Chironomoidea (Hennig 1981). The amphipneustic system is the most common condition in Diptera and is characteristic of larvae of Tanyderidae, Axymyiidae, most Psychodidae, Trichoceridae, Thaumaleidae, Anisopodidae and most Brachycera (Teskey 1981). Cranston *et al.* (1987) have interpreted the metapneustic condition in species of *Archaeochlus* Brundin as primitive for Chironomidae; however, it seems that their conclusions may be based on a misinterpretation of the spiracular system of larval Thaumaleidae (which they considered metapneustic). All species of *Thaumalea* Ruthe are amphipneustic, as are species of *Trichothaumalea* Edwards, and *Androprosopa* Mik (Lindner 1930, Teskey 1981). I am not aware of any reports of the spiracular system of *Austrothaumalea* Tonnoir, although that author (1927) indicates that the larva is similar to those of other thaumaleids. The larva of *Afrothaumalea* Stuckenberg has yet to be discovered (Stuckenberg 1961). Remm (1975) has concluded that the apneustic condition in Ceratopogonidae (the probable sister taxon of Chironomidae) is primitive for that family. Since *Archaeochlus* is apparently the only chironomoid genus whose members possess the metapneustic condition, it seems more likely that the character is a synapotypy of that genus alone. This interpretation would refute the conclusion of Cranston *et al.* (*loc. cit.*) that the primitive larval habitat for Chironomidae is eurythermic and hygropetric, rather than cold stenothermic in lotic waters (*cf.* Brundin 1966). The metapneustic condition in *Archaeochlus* is probably an adaptation to an environment subject to periodic drying, and would permit the larva to breathe atmospheric oxygen. Spiracular arrangements are obviously homoplastic in larval Diptera, and so caution should be exercised in interpreting groundplan states. A summary of the spiracular systems of larval Culicomorpha is diagramed in figure 2, with hypothesized groundplan states indicated at each internode of the dendrogram.

Wood (1978) provided further evidence for the sister-group relationship between Thaumaleidae and all other Chironomoidea by showing that spermatophore formation and transfer is characteristic of Simuliidae, Ceratopogonidae, and Chironomidae, but of no other Nematocera. Relationships among these latter three families are not as clear, although a sister-group relationship is suggested between Simuliidae and Ceratopogonidae + Chironomidae (Hennig 1981, Wood 1978). This interpretation seems to be the most reasonable at present, and is accepted here. A summary of the relationships discussed above is presented in figure 1.

The hypothesis of a close relationship between Simuliidae and Chironomidae has been advanced by several authors (Shewell 1958, Davies 1965a, Rubtsov 1974). However, such hypotheses must be based on purely phenetic grounds, for most characters shared between the two families are symplesiotypic.

The following discussion of simuliid groundplan apotypies is based on out-group relationships as discussed above. I take as the primitive out-group Ptychopteridae, Culicoidea, and Thaumaleidae; and as the derived out-group Ceratopogonidae and Chironomidae. Simuliid apotypies enumerated below without comment have already been discussed elsewhere, and are simply followed by the appropriate citation, and an indication about the hypothesized primitive state. The symbol (p) indicates characters that are judged to be primary synapotypies; (s) indicates secondary synapotypies.

2.7.1 The adult groundplan: Apotypies

Character 1 (s).

Pedicel (ped) reduced, not much wider than first flagellomere (flgm 1), cylindrical, similar in both sexes. — (Wood and Borkent 1982) (figs 40, 45). The primitive state is for the pedicel to be large relative to the flagellomeres.

Character 2 (s).

Form of antennal flagellum. — Although flagellomere number in Simuliidae varies between 7 (in species of *Twinnia*, *Gymnopais*, and some *Prosimulium*) and 10 (in certain species of *Simulium s.lat.*), I concur with Hennig (1973) that the basic number for the family is 9 (fig. 40). This is because 9 flagellomeres is the most commonly and widely encountered condition among simuliid genera. Ten flagellomeres are present in Thaumaleidae, and 13 each in Culicidae, Chaoboridae, and most Ceratopogonidae (11-12 in females of *Leptoconops* Skuse) (Borkent *et al.* 1987). Fourteen flagellomeres are present in Dixidae. Flagellomere number in Chironomidae varies between 1 and 15; however, it appears that the majority of genera are characterized by 13 or more flagellomeres in the male. The relatively small number of flagellomeres in Simuliidae must therefore be considered derived with respect to most other Culicomorpha. At least two other apotypic features of the simuliid flagellum are evident: the flagellomeres are generally shorter, broader, and more closely appressed than in related families (giving the antenna its characteristic thickset appearance); and the flagellum of males lacks the whorls of long setae characteristic of males of other Culicomorpha (Wood and Borkent 1982) (fig. 45).

Character 3 (p).

Wing greatly broadened at base. — Black flies are unique among Culicomorpha in having the wing greatly broadened at its base (fig. 9). In this respect, the wing resembles that of the distantly related Blephariceridae and Deuterophlebiidae (Hennig 1973). A greatly broadened wing base is evidently an adaptation of rheophilic insects whose pupae are bound to the substrate beneath the water. It presumably allows the newly emerged adult to unfold its wings very rapidly upon arrival at the water surface (Hennig *loc. cit.*).

Character 4 (s).

A small but distinct basal medial (bm) cell. — I cannot agree with the interpretation of Hennig (1973) that crossvein m-cu (tb) is absent from Simuliidae. This crossvein, which forms the apical margin of the bm cell, arises close to the wing base of most black flies (fig. 9). The consequence of such an arrangement is a small, but in most genera distinct, bm cell. The groundplan condition for Culicomorpha is for the bm cell to be much larger, with crossvein m-cu arising more apically on the wing (at or near the level of crossvein r-m). This latter condition is basic to Dixidae, Chaoboridae, Culicidae, Thaumaleidae, and Chironomidae; although secondarily lost in some lineages. The small bm cell in Simuliidae (absent from some genera) is derived with respect to these families. The condition in Ceratopogonidae is further derived in lacking crossvein m-cu altogether.

Character 5 (p).

Claw of male with comb-like spines on dorsal side at base. — (Wood and Borkent 1982) (fig. 41). The claw of other male Culicomorpha is simple apically.

Character 6 (p).

Hind tarsomere I (= hindbasitarsus) laterally flattened and ventrally keeled. — (Wood and Borkent 1982) (fig. 62). The plesiotypic condition is for the hindbasitarsus to be more cylindrical.

Character 7 (p).

Tergum I of abdomen with posterior fringe of long hairs (= basal fringe) on each side. — (Wood and Borkent 1982) (fig. 42). No such fringe is evident in any other Nematocera.

Character 8 (s).

A single large median spermatheca, with retention of the two lateral ducts. — (Wood and Borkent 1982) (fig. 10). Three spermathecae are present in the Diptera groundplan.

Character 9 (s).

Feeding behavior of adult female. — There are at least two major differences between the blood-feeding behavior of black flies and that of other haematophagous Nematocera. First, blood-feeding in the simuliid groundplan is strictly diurnal[6]; in Culicidae, Ceratopogonidae and Phlebotominae, feeding may occur nocturnally as well. Second, black flies spend a relatively long period of time crawling and probing before biting a host; females of Culicidae, Ceratopogonidae and other haematophagous Diptera bite very rapidly upon settling (Rubtsov 1969). Both of these characteristics may be interpreted as derived in Simuliidae. I disagree with the interpretation of Rubtsov (1974) that simuliids are primitively autogenous. There are relatively few species whose females are incapable of taking a blood meal, and their mouthparts are very similar to those of anautogenous species, except that their mandibles and maxillae are weakly developed (Nicholson 1945).

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[6] Females of ornithophilic species of black flies may feed nocturnally as well, but I consider this to be a secondarily derived feature of Simuliidae.

2.7.2 The pupal groundplan: Apotypies

Character 10 (p).

Respiratory organ (r.o.) with a "basal fenestra" laterally. — Most simuliids have a circular or oval-shaped area of very thin cuticle near the lateral base of the r.o. (a structure here termed the basal fenestra) (figs. 11, 15, 33, 34). At the larval-pupal ecdysis, the basal fenestra bursts to allow water to enter the lumen of the r.o. The shape of the r.o. is thus rendered independent of variation in hydrostatic pressure (Hinton 1957). The r.o. of *Crozetia crozetensis* lacks a basal fenestra, but the greatly prostrate form of the r.o. suggests that the fenestra may have been lost from that species.

Character 11 (s).

Respiratory organ (r.o.) multibranched. — In its basic form, the r.o. of pupal Culicomorpha consists of a simple cuticular tube. A branched r.o. is found only among members of Simuliidae (figs. 7, 11) and some relatively derived lineages of Chironomidae (*e.g.* Chironomini and some Pseudochironomini; *cf.* Coffman 1979). However, it is clear that the condition in these two families has been derived independently. In the simuliid groundplan, a common r.o. base gives rise to 3 main branches, although secondary filaments may arise from these "primary trunks". Such a condition is found in at least some members of the following plesiotypic genera: *Parasimulium, Prosimulium s.lat., Twinnia, Gymnopais, Procnephia, Paracnephia* and *Mayacnephia*. The evolutionary transformations of the pupal r.o. of Culicomorpha is diagrammed in figure 15.

Character 12 (p).

Pupal spiracle with regulatory apparatus operated by pharate adult. — The pharate adult of simuliids can regulate the opening and closing of the pupal spiracle by moving an apodeme that bridges the pupal and adult cuticles (Hinton 1957) (fig. 33, ras). Among Diptera, only the Psychodidae possess a similar mechanism (Sachell 1948), but this is undoubtedly the result of convergence.

Character 13 (p).

Abdominal segments 3 or 4 - 8 with tergites and sternites widely separated by pleural membrane. — The abdominal tergites and sternites of most Culicomorpha are evidently fused to each other laterally (*i.e.* they are apparently undivided by pleural membrane). The groundplan for Simuliidae is to have a wide area of striate pleural membrane (pl mem) dividing abdominal segments 3 or 4 - 8. Such a condition is found in nearly all simuliid genera, including *Parasimulium* (fig. 39). The tergites and sternites of *Crozetia* are only narrowly separated by pleural membrane (Davies 1974, personal observation), but this is probably a secondary development, as inferred from other characters (see also discussion of character 46). Similarly, the ring-like appearance of pupal abdominal segment 3 in *Twinnia* and *Gymnopais* has been interpreted as a secondarily derived feature (see discussion of character 46 in chapter 3). The evolutionary transformations discussed above are diagrammed in figure 17.

Character 14 (p).

Pharate pupa feeds and spins its cocoon. — According to Hinton (1958), simuliids are unique among Diptera in that the pharate pupa is able to feed and spin its own cocoon. In nearly all other endopterygotes, feeding ceases after the larval - pupal apolysis, and it is the larva that spins the pupal cocoon.

2.7.3 The larval groundplan: Apotypies

Character 15 (s).

Supernumarary and unfixed number of larval instars. — The number of larval instars reported for Simuliidae varies from 4 to 9, depending on species (*e.g.* Yakuba 1960, Harrod 1964, Fredeen 1976, Craig 1975). However, because instar numbers can only be distinguished using sophisticated techniques (Colbo and Wotton 1981), early reports of only four instars are open to question. Most species so far investigated have either six or seven larval instars (Crosby 1974), and the groundplan for Simuliidae is probably in this range. Most other Nematocera have a fixed number (4) of larval instars (Hennig 1948). Four instars have been reported for Dixidae (Peters 1981), Culicidae (Wood *et al.* 1979), Chaoboridae (*e.g.* Borkent 1979), Chironomidae (Oliver 1981), and Ceratopogonidae (*e.g.* Chan and LeRoux 1971). The number of larval instars for Thaumaleidae has not been firmly established. Mandaron (1963) resolved between 15 and 20 instars for *Thaumalea testacea* Ruth larvae; and B. Sinclair (*in litt.*) found in the order of 8 or 9 instars for *T. americana* larvae. However, it is doubtful that this is indicative of the monophyly of Thaumaleidae + Simuliidae.

Character 16 (p).

Form of labrum and labropalatum. — As indicated by Craig (1974) and Wood (1978) the labral fan of Simuliidae is fundamentally the same structure as the "lateral palatal brush" of other nematoceran families (Dixidae, Culicidae, and Ptychopteridae) (fig. 12). Indeed, Wood (*loc. cit.*) has argued that the labral fan of these families are homologous, and thus is evidence of their common ancestory. Nevertheless, several independently derived features of the simuliid labrum are evident, and are discussed below:

a) *Reduced number of rows of labral-fan rays.* — The labral fan of Ptychopteridae and most Culicomorpha consists of many rows of numerous hairs. In

Simuliidae, the number of rows is reduced to three; the primary fan (pf), the secondary fan (sf), and the median fan (mf) (Chance 1970) (fig. 43).

b) *Intertorma with anteroventrally directed stem.* — The intertormal stem of simuliids does not have a homologue in other Nematocera (Craig 1974).

c) *Interdigitation of ventral fascicles of the posterior frontolabral muscles (61).* — According to Craig (1974) the interdigitation of the posterior frontolabral muscles of Simuliidae is apotypic in relation to the non-interdigitated condition of most Nematocera. This latter condition is also evident in larvae of *Twinnia* and *Gymnopais*, but probably as a reversal.

Character 17 (p).

Salivary glands large, folded. — Rubtsov (1969) drew attention to the extremely large salivary glands of simuliid larvae. These glands are perhaps the largest of any Nematocera relative to the size of the body. From the salivary meatus, the gland projects posteriorly to segment 7, whereupon it doubles back upon itself (Puri 1925). Secretions of the salivary glands are used for locomotion and for the production of cocoon silk. The glands also contain giant polytene chromosomes, the banding patterns of which can provide evidence of sibling species (Rothfels 1981).

Character 18 (p).

Bacteria-covered multiporous sensillum (bms). — This sensillum is situated ventral to the membranous antennal base of simuliid larvae (Craig and Batz 1982); it is also present in the larvae of *Parasimulium stonei* (Borkent and Wood 1986) and *P. crosskeyi* (fig. 25). Although Craig and Batz (*loc. cit.*) have suggested that the bms is a possible homologue of the Lauterborn's organ of chironomid larvae, the position and form of the former sensillum renders this interpretation unlikely. No homologue of the bms has been identified in any other Culicomorpha.

Character 19 (p).

Dorsal anus. — Hennig (1973) remarked on the presence of a dorsal anus in larval Simuliidae (fig. 12). The most common condition in Diptera is for the anus to be ventrally situated — although terminally situated in some Nematocera (Teskey 1981). But because of the terminal position of the simuliid posterior proleg, the anus has necessarily assumed a dorsal position. This is because the posteroventral region of the abdomen is closely appressed to the substrate, and is thus rendered unsuitable as a site for defecation. The anus of larval Thaumaleidae occupies a similar position so it is possible that a dorsal anus is part of the Chironomoidea groundplan. However, the condition in simuliids is exaggerated because of the intervention of the anal sclerite (as) between the anus and the posterior proleg (pp) (fig. 13) (see also discussion of character 21 below). I regard this latter state as being synapotypic for Simuliidae.

Character 20 (p).

Anal papillae of three lobes. — Simuliids are unique among Culicomorpha in possessing an odd number (3) of anal papillae (ap). The papillae are either simple, as in most simuliid genera (fig. 12), or bear many secondary branches or lobes, as is found in many species of *Simulium s.lat.* (fig. 13). All other culicomorph larvae, as far as I am aware, possess an even number (2 or 4) of simple anal papillae. Four is evidently the groundplan number for Culicomorpha. Anal papillae probably serve in osmoregulation (Rubtsov 1969).

Character 21 (p).

Anal sclerite. — The anal sclerite is visible as an X-, Y-, or subrectangular-shaped structure on the dorsum of abdominal segment nine (figs. 13, 31). Inserted on the sclerite are muscles that operate the posterior proleg (Grenier 1949, Barr 1982). No other culicomorph larva possess such a structure. The anal sclerite is absent from *Ectemnia*, but this is probably the result of loss.

Character 22 (p).

Hook rows of thoracic and posterior prolegs. — Simuliidae is the only family of Chironomoidea in which the hooks of the thoracic (fig. 14, 56) and posterior prolegs (fig. 13, 31, 32) are arranged in longitudinal rows. The hooks of prolegs of Thaumaleidae, Chironomidae, and Ceratopogonidae are variously and irregularly arranged, but not in the linear fashion of black-fly larvae. The condition in Simuliidae is regarded as apotypic (D.M. Wood, personal communication).

2.7.4 The Egg Groundplan: Apotypies

Character 23 (p).

Egg triangular, with a dorsal transverse bulge. — Borkent and Wood (1986) concluded that the triangular egg shape of Simuliidae is synapotypic for the family. The typical condition in Nematocera is for the egg to be oval or nearly cylindrical in outline.

2.8 The primary evolutionary lineages of Simuliidae

I recognize two basic lineages within Simuliidae, ranked in a formal classification as subfamilies: Parasimuliinae and Simuliinae. Within Simuliinae, the initial dichotomy is accorded the rank of tribe as follows: Prosimuliini and Simuliini. In this section I enumerate characters hypothesized as groundplan apotypies of these primary evolutionary lineages.

Each of the four lineages is treated on an individual basis, although the numbering of character states is consecutive between treatments. Numbers in the character analysis are the same as those used in the concluding cladogram. Arrangement of characters follows a structural, rather than a phylogenetic, sequence.

The distribution of character states among simuliid genera is summarized in Table 2.2. The plesiotypic state is denoted by the symbol **0**. Character transformations from the plesiotypic state are denoted as **1**, **2**, **3**, and so on, where character state **1** represents the initial intermediate stage of a transformation series, and subsequent numbers represent increasingly derived states. For some features, more than one character transformation has evidently evolved from the plesiotypic condition. The symbols **1′**, **2′**... or **1″**, **2″**... *etc*. are used to indicate such independently derived character transformations.

Each character state enumerated below is followed by an indication as to whether or not it is considered to be a primary phylogenetic indicator. The symbol (p) denotes a primary synapotypy; (s) denotes a secondary synapotypy. Character states discussed by Wood and Borkent (1982) receive little further comment, except for an explanation of the symbols used in Table 2.2.

2.8.1 Subfamily PARASIMULIINAE Smart

PARASIMULIINAE Smart, 1945: 479. Type-genus: *Parasimulium* Malloch, 1914.

Peterson (1977) provided a diagnosis of Parasimuliinae based on features of the adult male. The following diagnosis expands on his definition, and includes features of the female, pupa, and larva. The diagnosis of the immature stages may have to be amended in light of future discoveries.

Diagnosis. *Male and Female*: Branches of Rs widely separated by membrane; R_1 connected to C slightly before middle of wing; R_{4+5} connected well before terminus of C; C, Sc, and Rs with long setae; false vein (m-cu fold) simple apically; CuA_2 only slightly sinuous. Katepisternum rudimentary, almost pointed ventrally in profile; katepisternal sulcus absent. Mesepimeral tuft absent. Calcipala and pedisulcus absent. *Male*: Eye with facets similar in size (except few large facets anteromedially); eyes widely separated at vertex (dichoptic), nearly in contact below antennae. Gonostylus without apical peglike seta. *Female*: Sternum X undivided medially. *Pupa*: Plastron network only on branches of respiratory organ (absent from elongate common base of respiratory organ); felt chamber evident in base of respiratory organ, as internal membranous continutation of mesothoracic spiracle, terminated near origin of respiratory organ branches; mesothoracic spiracle communicating with lumen of respiratory organ. Abdominal segment 3 complete (ring-like), undivided by pleural membrane. Sternites 6 and 7 undivided medially by a longitudinal area of striate membrane. Pleuron without recurved hooks. Tergites without anterior row of posteriorly directed spines (spine-combs). *Larva*: Antenna of 1 article. Postgenal cleft absent. Lateral plate of prothoracic proleg absent. Abdominal segment 8 with single, large, conical lobe ventrally. Anal sclerite with ventral arms not articulated with median sclerite dorsally; apices of ventral arms nearly in contact midventrally, separated by small, spindle-shaped sclerite (ventromedian sclerite).

The single genus in the subfamily, *Parasimulium*, is recorded only from the western Nearctic region. It comprises 4 species in two subgenera: *Parasimulium s.str.* (3 species) and *Astoneomyia* (1 species). The monophyly of the subfamily is uncertain at present, and will remain so until additional material of *Astoneomyia* is collected (Wood and Borkent 1982). However, at this time, I consider the genus to be monophyletic. Character states 26 - 30 have been confirmed for species of both *Astoneomyia* and *Parasimulium s.str.*; all other characters in this section have so far only been confirmed for species of *Parasimulium s.str.*

The adult groundplan: Apotypies

Character 24 (s).

Stemmatic bulla. — Species of *Parasimulium s.str.* share with those of *Gymnopais* and *Twinnia* a shiny raised stemmatic bulla (sb) near the posterior margin of the compound eye (**1**) (fig. 44). Such a structure may be found in *Astoneomyia*, but the head of the only known specimen is missing. All other simuliids lack a prominent bulla (**0**) (fig. 49), although one is suggested in some species of *Prosimulium s.str.* and *P. (Helodon)* (Wood 1978). The only other flies with a similar structure are the nymphomyiids (Kevan and Cutten 1981) and some aberrant Chironomidae (Oliver 1981). The presence of a bulla is correlated with reduction of the compound eye (McAlpine 1981), and has undoubtedly arisen several times independently in Diptera. In Simuliidae, a prominent stemmatic bulla has evidently evolved at least twice: once in *Parasimulium*, and once in the *Twinnia* - *Gymnopais* clade. The bulla is thought to be the remnant of the larval eye.

Character 25 (s).

Antennal flagellum of 8 articles. — As discussed under the section on simuliid groundplan apotypies (character 2) the basic flagellomere number for adults is presumed to be 9 (**0**). Thus, the occurrence of only 8 flagellomeres in *Parasimulium s.str.* is considered apotypic (**1**) (fig. 45). Other simuliids possessing an 8 articled flagellum include species of *Austrosimulium*, *Paraustrosimulium*, and isolated species of *Prosimulium s.lat.*, *Greniera*, and *Simulium s.lat.* This regressive condition has undoubtedly evolved several times independently in Simuliidae, and thus is not convinving evidence of the monophyly of *Parasimulium s.str.* The condition in *Astoneomyia* is unknown. Other character states in Simuliidae are as follows: 7 flagellomeres (**2**), 10 flagellomeres (**1'**).

Character 26 (s).

Katepisternum markedly reduced, almost pointed ventrally in profile. — (Wood and Borkent 1982). The apotypic state is **1** (fig. 46); the plesiotypic state, a katepisternum that is much more convex ventrally, is **0** (fig. 50). Because the apotypic state is a reduction, it cannot be taken as primary evidence of the monophyly of *Parasimulium s.lat.*

Character 27 (s).

Mesepimeral tuft lost. — (Wood and Borkent 1982). The apotypic state is **1** (fig. 46); the plesiotypic state, which is for a tuft of seta to be present on the dorsal part of the mesepimeron, is **0**. Loss of the tuft cannot be taken as primary evidence of the monophyly of *Parasimulium s.lat.* as such a condition is regressive and subject to homoplasy.

Character 28 (s).

Basal medial (bm) cell lost. — A small, distinct bm cell is commonly and widely distributed among simuliid genera (fig. 9). As discussed under character 4 such a condition is interpreted as part of the simuliid groundplan (**0**). Absence of this cell must therefore be considered derivative (**1**) (fig. 20), and is evidence of the monophyly of *Parasimulium s.str.* + *Astoneomyia*. However, a regressive bm cell is also found in other lineages of black flies (*Gigantodax*, *Simulium s.lat.*) and in itself does not provide strong evidence of the monophyly of *Parasimulium s.lat.*

Character 29 (s).

Basal radial (br) cell reduced in length. — A relatively long br cell is evidently part of the culicomorph groundplan, at least as inferred from the distribution of this character throughout the infraorder. In Culicoidea, the br cell is equal to about one-half the length of the wing as measured from the base of the cell. In Chironomoidea, the cell is rather varied in length, and has evidently become reduced through convergence a number of times. Two length categories of the br cell are recognized in Simuliidae: one, in which the br cell is equal to about one-third the length of the wing as measured from the base of the cell (fig. 9); and another, in which the cell is less than one-quarter that length. Because the former condition is widespread among simuliids, and most closely approximates the condition found in Culicoidea, I regard it as being plesiotypic (**0**). A derived (shortened) br cell (**1**) is characteristic of *Parasimulium s.str.*, *Astoneomyia*, and at least two other simuliid lineages (*Austrosimulium*, *Simulium s.lat.*). But based on other characters, the condition in *Parasimulium s.lat.* is clearly independently derived from the others (fig. 20). This character is not convincing as a synapotypy because it is regressive and subject to homoplasy.

Character 30 (s).

Gonostylus with apical peglike seta lost. — (Wood and Borkent 1982). The apotypic state is **1** (fig. 47); the plesiotypic state, a gonostylus with one or more setae, is **0**. The seta has evidently been lost from various other lineages of Culicomorpha, including Simuliidae (*Simulium* subgenus *Shewellomyia* Peterson). This character is therefore only taken as secondary phylogenetic evidence.

Character 31 (s).

Mating behavior. — Wood and Borkent (1982) provided a detailed description of the mating behavior of *P. crosskeyi*. Virgin females rest motionless on the undersides of leaves while males search underneath such leaves for prospective mates. This same behaviour has subsequently been observed for *P. stonei* (D. M. Wood, personal communication; personal observation). The typical culicomorph condition (as in most other Diptera — *cf.* McAlpine and Munroe 1968) is for the male to form aerial aggregations (swarms), into which the female flies to become mated (**0**). The mating behavior of *Parasimulium* is probably apotypic for Simuliidae (**1**); however, the majority of genera have yet to be surveyed for this character. Character state **1′** denotes simuliids that mate on the ground, such as species of *Gymnopais*, *Cnephia dacotensis* (Dyar and Shannon), and *Simulium decorum* Walker. Until more is known about the mating behaviour of Simuliidae, character state **1** can only be taken as a secondary phylogenetic indicator.

Character 32 (s).

Autogenous females. — As discussed under character 9 adult females of Simuliidae are presumed to be primitively anautogenous (**0**). Their mouthparts agree in many important features with those of the following Diptera, which also have blood-sucking representatives: Blepharoceridae, Psychodidae, Culicidae, Chaoboridae (*Corethrella*), Ceratopogonidae, Tabanidae, and Rhagionidae (Downes 1958, Borkent *et al.* 1987). Although the feeding behaviour of most simuliids has yet to be determined, the likelihood of blood feeding can be inferred from the structure of the mouthparts. Species that have well developed teeth on the mandibles and laciniae are presumed to be blood feeders, whereas species that lack such armature are presumed to be incapable of piercing the skin (Krafchik 1942, Nicholson 1945). On this basis, females of *Parasimulium* are presumed to be autogenous (**1**). The symbol "?" is used to indicate character states that were determined solely with reference to the structure of the mouthparts (Table 2.2). The apotypic state cannot be taken as a primary phylogenetic indicator because autogeny has evidently evolved a number of times independantly in Simuliidae. All species of *Gymnopais* are autogenous, as are isolated species of many other genera.

The preimaginal groundplan: Apotypies

Character 33 (s).

Maxillary palpus of first-instar larva with subapically arranged sensilla. — Borkent and Wood (1986) provided a description of the maxillary palpus of first-instar *Parasimulium stonei*. Instead of the typical culicomorph condition, in which the sensilla are apically postioned and in a circular configuration (**0**) (Craig and Borkent 1980), the sensilla are subapically situated on the palpus, although still in the typical circular arrangement (**1**). The condition in first-instar *Parasimulium* was interpreted by Borkent and Wood (*loc. cit.*) as an intermediate stage of a transformation series between the usual culicomorph condition (as in most simuliid genera examined; *e.g.* fig. 30), and the laterally-positioned-but-linear-arrangement of sensilla in first instars of *Prosimulium*, *Twinnia*, and *Gymnopais* (**1′**) (fig. 60). In the present analysis, I regard the condition in *Parasimulium* as independently derived. The arrangement of palpal sensilla in first-instar *Astoneomyia* is unknown. Character state **1** can only tentitively be considered a synapotypy of *Parasimulium s.lat.*, as the majority of simuliid genera have yet to be surveyed for this character.

Character 34 (s).

Abdominal segment 8 of larva with a single, large, conical lobe ventrally. — In the chironomoid groundplan, the venter of abdominal segment 8 is simple (*i.e.* there are no obvious projections or extensions of the abdominal cuticle at that point). A simple segment 8 is probably also part of the groundplan for Simuliidae (0), as inferred from the occurrence of such a condition in the following plesiotypic taxa: *Prosimulium, Levitinia, Twinnia, Gymnopais, Procnephia, Paracnephia, Crozetia,* the Australian "*Cnephia*", and most Neotropical "Prosimuliini" *sensu* Wygodzinsky and Coscarón (1973). The larva of *Parasimulium crosskeyi* is derived with respect to other simuliids in having a single large tubercle or lobe (mvt) on the venter of abdominal segment 8 (1) (fig. 48). The only other simuliid having a similar structure is the larva of *Stegopterna*. However, the "single, transverse, midventral bulge" of this latter genus is probably not homologous with the structure in *Parasimulium*, as judged from other characters (1´). Similarly, the paired, conical, ventral tubercles (1´´) of certain other genera (*Mayacnephia, Lutzsimulium, Austrosimulium, Greniera, Ectemnia,* and some *Simulium s.lat.*) are probably independently derived (fig. 12). Character state 1 is here considered a secondary synapotypy of *Parasimulium*.

Character 35 (p).

Hypogean habitat. — I have argued that the habitat of immature *Parasimulium* is not hyporheic, as suggested by Courtney (1986), but is rather hypogean or phreatic. Although the differences between these two types of habitats may appear trivial, and in fact may be difficult to distinguish where they occur together, there remains observable biological differences between them (*i.e.* there are elements that occur in the seep that do not occur in the main stream, and *vice versa*). If the proposition is accepted that the immature stages of *Parasimulium* are truely hypogean, then the habitat is clearly unique for

Simuliidae (1), and perhaps even for Diptera. But even if the immatures prove to be hyporheic, then the distinction must still be drawn between the apparent obligatory existence of *Parasimulium* in that habitat, and the facultative occurrence of other simuliids (Currie and Craig 1987). The groundplan condition for black flies is clearly for the immatures to be attached to exposed substrates in surface-flowing streams (0). Character state 1 is taken as primary evidence of the monophyly of *Parasimulium s.str.*

Character 36 (s).

Lack of pigmentation. — Larvae of *Parasimulium crosskeyi and P. stonei* are apparently blind and almost completely unpigmented (except for the heavily sclerotized anterior margin of the hypostoma) (fig. 9). The pupal integument of *P. crosskeyi* is almost completely transparent, revealing the developing adult underneath. These adaptations are clearly associated with the subterranean environment of the immatures (1). Among Culicomorpha, only larvae of Chaoboridae (in part) are translucent or transparent; however, the groundplan for that family is evidently for the larva to be darkly colored (Sæther 1970). The immatures of all other simuliids have at least some pigmentation, and two of the three pairs of larval ocelli (stemmata) are darkly pigmented (Nyhof and McIver 1987) (0). Lack of pigmentation is a regressive feature, and therefore may be considered only a secondary indicator of the monophyly of *Parasimulium s.str.*

Systematics of Parasimuliinae

The monophyly of *Parasimulium s.lat.* is supported by at least 5 characters (characters 26 - 30) (fig. 6). As many as 8 additional characters may also be synapotypic for the genus (characters 24, 25, 31 - 36), but this can only be confirmed through discovery of the female and immature stages of *P. furcatum* and *P. melanderi*. Although none of the 5 confirmed synapotypies can be considered a primary phylogenetic indicator, they do, in combination, represent moderately convincing evidence of the monophyly of the genus.

One of the most curious features of *Parasimulium s.lat.* is the arrangement of wing veins. The primitive status of the genus has largely been inferred by the widely separated branches of the radial sector. However, several derived features of the wing are also evident, such as loss of the bm cell (Character 28), and reduction of the br cell (Character 29). Such discord raises questions about the direction of character evolution in the simuliid wing. D. M. Wood (*in litt.*) has raised the possibility that a widely branched radial sector in simuliids is actually a reversal toward the culicoid condition, and thus is evidence of the common ancestory of *Parasimulium* + *Prosimulium s.lat.* + *Twinnia* + *Gymnopais*. This hypothesis is based on the presence of a rather shortly branched radial sector in the groundplan of Thaumaleidae, Ceratopogonidae, and Chironomidae. Evidence for a close relationship between *Parasimulium* and some typical members of the Prosimuliini *sensu* Crosskey has already been forwarded based on larval characters (Borkent and Wood 1986), and although this hypothesis cannot be dismissed out of hand, I believe that other evidence will show that *Parasimulium* is only distantly related to other black flies. I have therefore retained the traditional view that a widely branched radial sector is primitive for Simuliidae, and that a shortly branched- or unbranched radial sector represents increasingly derived states respectively (fig. 20). The phylogenetic relationships of *Parasimulium* to other simuliids is discussed later in this chapter.

The phylogenetic significance of the anal sclerite of larval *Parasimulium* remains uncertain. Of particular interest are the ventral arms (va), which are not articulated dorsally with the dorsomedian sclerite (dms). Ventrally, the ventral arms almost meet along the midline, and are separated only by a small, spindle-shaped sclerite (ventromedian sclerite, vms) (fig. 31). No other simuliid that I am aware of has such an arrangement. In *Crozetia* larvae the apices of the ventral arms almost meet midventrally, but like all other simuliids they are articulated dorsally with the dorsomedian sclerite. Also, the ventromedian sclerite is lacking in *Crozetia*. In most other simuliids the ventral arms are considerably shorter than in *Parasimulium* and *Crozetia*, and they project ventrally to a point no farther than about one-half the distance round abdominal segment IX (fig. 13). Whether the short- or long-arm state represents the primitive condition for Simuliidae cannot be determined using out-group comparison, and the distribution of these states within the family sheds little light. The condition in *Parasimulium* and *Crozetia* should not be confused with that in certain other simuliids (*Gigantodax*, *Austrosimulium* [in part] and *Simulium s.lat.* [in part]), in which a "semicircular sclerite" contours the ventral half of abdominal segment X (Dumbleton 1962). The semicircular sclerite is a separate structure (although probably serving as an accessory to the anal sclerite), and has probably developed along its own lines several times independently.

Despite incomplete knowledge of all life-history stages of *Parasimulium* it is important to forward an initial hypothesis about relationships among species. The following discussion is based on male characters only, with each character being indicated by a letter. These same letters appear on the cladogram (fig. 6).

I concur with Wood and Borkent (1982) that *Astoneomyia* and *Parasimulium s.str.* are probable sister taxa; and hence, *P. melanderi* is placed as the sister group of all other *Parasimulium*. Synapotypic characters of *Parasimulium s.str.* include (a) supra-alar notch narrow and deep, (b) gonocoxite with apicolateral finger-like extension, (c) ventral plate with forked apex, (d) median sclerite long and strap-like, with apically widened portion, and (e) gonostylus with subapical cusp ("inner gonostylus") on dorsal side. A detailed discussion of these characters has already been provided by Wood and Borkent (1982). Although I have not examined material of *P. furcatum* first hand, it would appear that it is less closely related to the other 2 species of *Parasimulium s.str.* than they are to each other.

If the original description of Malloch (1914) is correct, then the following characters can be taken as synapotypic for *P. crosskeyi* and *P. stonei*: (f) scape yellow (black in *P. furcatum* and *P. melanderi*); and (g) tergites 1 and 2, and sternites 1-3 yellow (abdomen brown in *P. furcatum* except for tergum 1, which is yellow; abdomen entirely brown in *P. melanderi*).

2.8.2 Subfamily SIMULIINAE Newman

Simuliites Newman, 1834: 387. Type genus: *Simulium* Latreille, 1802.

Diagnosis: *Male and Female:* Rs unbranched, or with branches closely approximated; R_1 connected to C well beyond middle of wing; R_{4+5} (or R_{2+3} and R_{4+5} if Rs unbranched) connected near terminus of C; C, Sc, and Rs with short setae; false vein (m-cu fold) forked apically; CuA_2 markedly sinuous. Katepisternum long, rounded ventrally in profile; katepisternal sulcus present. Mesepimeral tuft present. Calcipala and pedisulcus present or absent. *Male:* Eye typically with line of discontinuity between large upper facets and small lower facets (absent from some species of *Gymnopais*); eyes typically in contact at centerline above antenna (holoptic). Gonostylus typically with one or more apical peglike setae (absent from *Simulium (Shewellomyia)*). *Female:* Sternum X divided medially. *Pupa:* Plastron held over entire surface of respiratory organ, including base; base of respiratory organ without felt chamber internally; mesothoracic spiracle in contact with lumen of thickened part of plastron on dorsal side of base (not with lumen of base). Abdominal segment 3 typically divided by pleural membrane (undivided in species of *Twinnia* and *Gymnopais*); sternites 6 and 7 (at least) divided medially by a longitudinal area of striate membrane; pleuron typically with recurved hooks; tergites typically with anterior row of posteriorly directed spines (= spine combs). *Larva:* Antenna of 3 articles. Postgenal cleft normally present (in some members represented only by wrinkling of cuticle in posteroventral region of the headcapsule). Lateral plate of prothoracic proleg present. Abdominal segment 8 simple, with pair of ventral tubercles, or with single, transverse, midventral bulge. Ventral arms of anal sclerite articulated with dorsomedian sclerite dorsally, their apices widely separated ventrally(if apices of arms closely approximated ventrally, then not separated by spindle-shaped sclerite).

The subfamily Simuliinae comprises all simuliid genera exclusive of *Parasimulium s.lat.* Its members are world wide in distribution, excluding Antarctica and some islolated oceanic islands. The monophyly of Simuliinae is supported by the 15 synapotypic characters enumerated below.

The adult groundplan: Apotypies

Character 37 (s).

Eye of male with line of discontinuity between large upper facets and small lower facets. — (Wood and Borkent 1982). The apotypic state is **1** (fig. 49); the plesiotypic state, which is for absence of such line of discontinuity, is **0** (fig. 45). The apotypic state is evident in several other families of Nematocera: Blephariceridae (in part), Axymyiidae, Bibionidae, and Cecidomyiidae (*Trisopsis* Kieffer). However, the condition is unknown in any other family of Culicomorpha, and must therefore be considered an independently derived feature of Simuliinae. Dichoptic males of *Gymnopais* have no evident line of discontinuity between the upper and lower eye facets, but are undoubtedly derived from an ancestor whose eyes were so divided. Indeed, the holoptic male of certain plesiotypic species of *Gymnopais* (*e.g. G. holopticus*) have a divided eye. The condition found in dichoptic Simuliinae males must therefore be considered a further derived state (**2**). Because of the instances of homoplasy described above, the derived state can be taken only as secondary phylogenetic evidence. The function of the "dorsal eye" of male Diptera is to detect small, rapidly moving females against skylight as they fly above swarms of males (Kirschfeld and Wenk 1976, Zeil 1983, O'Grady and McIver, 1987).

Character 38 (s).

Radial sector with branches (R_{2+3} and R_{4+5}) closely approximated. — (Wood and Borkent 1982). the apotypic state is **1**; the plesiotypic state, which is for the branches of the radial sector to be more widely separated, is **0**. A summary of the hypothesized transformations is given in figure 20. The derived state can be taken only as secondary phylogenetic evidence because it is a reduction. This character is considered in greater detail in the discussion of character 58.

Character 39 (p).

False vein (m-cu fold) forked apically. — Simuliidae, Ceratopogonidae, and Chironomidae are the only Culicomorpha having a false vein between the posterior branch of M and CuA_1. This can be taken as further evidence of the common ancestry of these three families. A simple or unbranched false vein is characteristic of Ceratopogonidae and Chironomidae; but among simuliids, only *Parasimulium s.str.* and *Astoneomyia* are known to have such a condition (which must be considered basic to these three families)(**0**). The derived condition, a false vein that is forked apically, is characteristic of all other simuliids, and can be taken as primary phylogenetic evidence of the monophyly of Simuliinae (**1**). The hypothesized transformation is illustrated in figure 20.

Character 40 (s).

Katepisternal sulcus (mesepisternal groove). — Most simuliids have the katepisternum divided into a dorsal and a ventral part by a horizontal groove termed the katepisternal sulcus (**1**) (fig. 50) (McAlpine 1981). The only simuliids lacking this sulcus are species of *Parasimulium s. str.* and *Astoneomyia* — a condition shared by all other Diptera (**0**) (fig. 46). However, as indicated in the discussion of character 26, the katepisternum of *Parasimulium s.lat.* is reduced ventrally, so it is possible that the sulcus has become secondarily lost in that genus. If this were so, the katepisternal sulcus would have to be considered a synapotypy of the entire family. Until further evidence is brought to bear on the problem, the presence of a katepisternal sulcus can be considered only tentatively a synapotypy of Simuliidae, exclusive of *Parasimulium s.lat.*

Character 41 (s).

Sternum X of female divided medially. — (Wood and Borkent 1982). The apotypic state is **1**; the plesiotypic state, which is for sternum X to be incompletely divided in the female, is **0**. Wood and Borkent (*loc. cit.*) compared the completely divided sternum X of most simuliids (= anal lobe) with the undivided sternum of other Culicomorpha. They interpreted tentatively the condition in *P. crosskeyi* (which has sternum X deeply notched but narrowly continuous medially) as forming an intermediate stage of a transformation between the condition in other Culicomorpha, and that in all other Simuliidae. Examination of the female of *P. stonei* corroborates this conclusion, which is accepted here. However, it is still not clear as to whether the condition in *Parasimulium s.str.* is primitive for Simuliidae, or whether it represents a secondary fusion of the anal lobes. If this were so, the completely divided state would have to be considered a synapotypy of the entire family. Until further evidence is brought to bear on the problem, the derived state must be considered only a secondary phylogenetic indicator. A summary of the proposed transformations is given in figure 21.

The pupal groundplan: Apotypies

Hinton (1957, 1968, 1976) provided detailed accounts of the pupal respiratory organ (r.o.) of Simuliidae. Although varied in external appearence, the r.o. has the same basic structure and function throughout the family. However, at least 3 derived features of the r.o. are evident in Simuliidae, exclusive of *Parasimulium*. These are individually discussed below. Those unfamiliar with the structure of the simuliid respiratory organ are referred to the references given above. Figures 15 and 16 illustrate some of the transformations discussed under characters 42 through 44 below.

Character 42 (þ).

Plastron network covering the entire respiratory organ (r.o.). — According to Hinton (1976), Simuliidae and Chironomidae are the only Culicomorpha in which a plastron (or spiracular gill) is held on the pupal r.o. However, examination of the pupa of *Thaumalea americana* reveals that a spiracular gill is also present in Thaumaleidae. Although Hinton (1968) considers the plastron to be independenly derived in most families of Diptera, it can also be argued that a plastron is part of the chironomoid[7] groundplan. This is the interpretation followed in the present work. In Thaumaleidae and primitive Chironomidae (Telmatogentoninae, Tanypodinae, Podonominae, and Aphroteniinae), the plastron (= plastron plate) is restricted to the apex of the r.o. A similar condition is found in the pupa of *Parasimulium crosskeyi*, in which the plastron is held on the three branches of the r.o., but not on the elongate r.o. base (0) (figs. 33 - 35). In all other simuliids, at least as far as I am aware, the plastron covers the entire r.o., including the base. Such an arrangement is clearly unique among Culicomorpha and can be taken as primary evidence of the monophyly of Simuliinae (1). I interpret the condition in *Parasimulium* as forming an intermediate stage of a transformation series between the plaston plates of other Chironomoidea (which must be considered primitive), and the extensive plastron network of all other Simuliidae (figs. 15, 16 i, 16 ii).

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[7] The respiratory organ of Ceratopogonidae apparently lacks a plastron network, but this may be interpreted as a loss.

Character 43 (s).

Felt chamber of respiratory organ lost. — The felt chamber is the internal component of the culicomorph pupal r.o., a tubular continuation of the mesothoracic spiracle. It is formed by the dorsolongitudinal invagination of the r.o., as suggested by the presence of an external longitudinal scar along the dorsal surface of the the r.o. base (fig. 34). Internally the chamber is clothed with a dense series of fine hairs, which evidently serve to reduce water loss during periods of drought. A felt chamber is visible in the r.o. of Dixidae, Chaoboridae, Culicidae[8], Thaumaleidae, Ceratopogonidae, and Chironomidae. To date, *Parasimulium crosskeyi* is the only simuliid known to have such a structure (figs. 33, 34). A felt chamber may eventually prove to be characteristic of *Parasimulium* as a whole, but this can be confirmed only through additional discoveries. The condition in *P. crosskeyi* is clearly primitive as judged from out-group comparison (0). Absence of a felt chamber must therefore be derived (1), and can be taken as evidence of the monophyly of Simuliidae, exclusive of *Parasimulium* (figs. 15, 16 ii). Because the apotypic state is a regressive feature, it can only be considered a secondary phylogenetic indicator.

Character 44 (p).

Pupal spiracle communicating with "lumen" of plastron. — In the Culicomorpha groundplan (as in most other aquatic Nematocera) the mesothoracic spiracle communicates directly with the base of the r.o. Such a condition is characteristic of Dixidae, Chaoboridae, Culicidae, Thaumaleidae, and Ceratopogonidae. Coffman (1979) reported the same pattern in the following plesiotypic lineages of Chironomidae: Tanypodinae, Podonominae, Aphroteniinae, and Telmatogetoninae. Among Simuliidae only *Parasimulium crosskeyi* has the mesothoracic spiracle communicating directly with the lumen of the r.o. (**0**) (fig. 33). In other simuliids the spiracle is somewhat more dorsally situated, communicating directly with the thickened area of plaston on the dorsal base of the r.o. (Hinton 1957). This latter condition appears to be unique and is here considered a primary synapotypy of Simuliinae (**1**) (figs. 15, 16 ii).

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[8] The felt chamber of Culicidae closely approximates the inner surface of the r.o., and is therefore not visible externally as in other Culicomorpha.

Character 45 (p).

Sternites 6 and 7 (at least) divided medially by a semi-membranous longitudinal striate area. — In almost all simuliid pupae, sternites 6 and 7 are divided along their midline by a longitudinal tract of striate membrane. This division is also evident in some specimens on sternites 5 and 8, although not as conspicuously. Even in members of Simuliini *sensu* Crosskey (1969) (*i.e. Austrosimulium, Metacnephia, Simulium s.lat.*), which are widely reputed to have sternites 6 and 7 entire (*e.g.* Wygodzinsky and Coscarón 1972; *cf.* key to pupae, pg. 142), the division may in fact be resolved with the aid of a compound microscope. The condition is merely obscured in such taxa because the pupal abdomen is very weakly sclerotized, making the distinction between sternite and membrane difficult. The pupa of *Parasimulium crosskeyi* lacks any suggestion of a mediolongitudinal division of sternites 6 and 7, which is the condition found in all other Culicomorpha (**0**) (fig. 39). The divided state (**1**) therefore may be considered a primary synapotypy of Simuliidae, exclusive of *Parasimulium* (fig. 51). The transformations discussed above are illustrated in figure 19.

Character 46 (s).

Abdominal segments 3 - 8 with terga and sterna divided by pleural membrane. — As discussed under character 13, simuliid pupae are unique among Culicomorpha in having a wide area of pleural membrane dividing abdominal segments 3 or 4 - 8. The lesser number of divided segments (4 - 8) (**0**), such as found in the pupa of *Parasimulium crosskeyi*, is hypothesized to form an intermediate stage of a transformation series between the entirely undivided state, as found in all other Culicomorpha, and the more completely divided conditon (3 - 8), in the majority of simuliid genera (**1**). Besides *Parasimulium*, the only other simuliids having a ring-like segment 3 are the pupae of *Twinnia* and *Gymnopais*. However, these genera are believed to be derived from a *Prosimulium s.lat.* ancestor (Wood 1978), and so the condition must be interpreted as secondarily derived (**2**). The pupa of *Crozetia* has segments 3 - 8 divided only narrowly by pleural membrane, but this is probably an independent modification from the Simuliinae groundplan (**2´**). Because of the instances of homoplasy discussed above, character state **1** can be taken only as secondary phylogenetic evidence. A summary of the transformations discussed above is given in figure 17.

Character 47 (s).

Pleuron of abdominal segments 6 and 7 (at least) with recurved hooks and plates (pleurites). — In most simuliid pupae, the pleura of segments 6 and 7 (at least) possess one or more recurved hooks on each side (fig. 52). The hooks resemble those on the adjacent sternite, and may or may not be associated with a pleurite. Pleurites, too, are present in most simuliid pupae, but not necessarily in association with the hooks. In taxa that are characterized by a weakly sclerotized pupal abdomen (*Austrosimulium, Metacnephia, Simulium s.lat.*), it may be difficult to determine whether the hooks arise from the pleuron or the sternum; however, magnification under a compound microscope makes the distinction possible. The only simuliids without pleural hooks or conspicuous pleurites are *Parasimulium crosskeyi* (fig. 39) and *Greniera* (this latter as judged from *G. denaria* Davies, Peterson, and Wood). The condition in *Greniera* is probably secondary, as judged from other characters. Absence of pleural hooks and pleurites in *Parasimulium* may be interpreted as an intermediate stage of a transformation series between the condition found in most Culicomorpha (in which the tergites and sternites are fused together laterally), and the condition found in most other simuliids (in which pleural hooks and pleurites are presumed to be uniquely derived). That is, it is hypothesized that the wide area of pleural membrane developed first in Simuliidae (**0**), followed by secondary development of pleural hooks and pleurites (**1**). Loss of such sclerotized features of the pleural membrane is denoted by **2**. Character-state **1** can be taken only as a secondary synapotypy because of homoplasy. A summary of the hypothesized transformations is given in figure 17.

Character 48 (s).

Abdominal tergites 4 or 5 - 9 each with an anterior row of posteriorly-directed spines. — Most genera of black flies have the anterior margin of abdominal tergites 4 or 5 - 9 with a single row of posteriorly directed spines (= spine combs) (figs. 52, 53). The condition in the pupa of *Parasimulium crosskeyi* is similar to that of other Culicomorpha in lacking such spine combs (spines, in fact, occur on the abdominal tergites of many Culicomorpha pupae, but their position and form renders homology with the simuliid spine combs unlikely). Because spine combs have evidently evolved very early in black flies — as inferred by their presence is such plesiotypic taxa as *Prosimulium, Procnephia, Paracnephia,* the Australian "*Cnephia* ", and most Neotropical "Prosimuliini" *sensu* Wygodzinsky and Coscarón (1973) — it is tempting to consider their absence from *Parasimulium* as plesiotypic. One difficulty with this interpretation is that the spine combs are subject to reduction or loss. For example, pupal *Twinnia* and *Gymnopais* lack spine combs, but are clearly derived from an ancestor (*Prosimulium s.lat.*) that had them (Wood

1978). Thus, the question arises as to whether spine combs should be considered a groundplan feature of the entire family. In some taxa, the loss may be correlated with the reduction of the pupal cocoon (**2**) (*Twinnia, Gymnopais, Crozetia,* and *Tlalocomyia*); in others, it may be part of a trend towards desclerotization of the pupal abdomen (**2′**) (*Austrosimulium* and some species of *Simulium s.lat.*, esp. subgenus *Afrosimulium*). *Parasimulium* has neither a greatly reduced cocoon, nor an especially desclerotized abdomen. It seems possible therefore that the condition in *Parasimulium* is actually primitive (**0**), and not the result of loss. Because of homoplasy, character-state **1** can be considered only tentatively a synapotypy of Simuliidae, exclusive of *Parasimulium*. The transformation discussed above is diagramed in figure 18.

The larval groundplan: Apotypies

Character 49 (p).

Antenna of three articles. — Craig and Batz (1982) studied structural details of the simuliid larval antenna. The antenna of first-instar larvae consists of only a single article; at first moult, a basal article is added. In subsequent instars, the basal article becomes annulated to give the appearance of a three-articled antenna (fig. 54). In all larval instars of *Parasimulium* so far examined, the antenna consists of only a single antennal article[9] (Borkent and Wood 1986, personal observation) (fig. 7, 25). As a single antennomere is present in most other culicomorph larvae (Dixidae, Chaoboridae, Culicidae, Thaumaleidae, Ceratopogonidae), the condition is taken as primitive for Simuliidae (**0**). The three-articled antenna of later instars (**1**) may therefore be considered a synapotypy of the family, exclusive of *Parasimulium*. The only other culicomorph family with a multiarticled larval antenna is Chironomidae (4 - 7, typically 5); however, the basic structure of the antenna is much more complex in that family (*e.g.* presence of antennal blade, Lauterborn organ). As the condition in Simuliinae is not manifest in any other Culicomorpha, it is taken as primary phylogenetic evidence.

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[9] Courtney (1986) incorrectly interpreted the membranous antennal base of later instar *P. crosskeyi* larvae as being the basal two articles combined.

Character 50 (s).

Postgenal cleft. — The postgenal cleft (p clft) is a feature of the ventral surface of the simuliid larval head capsule. Comprised of thin, slightly sclerotized cuticle, the cleft occupies an area anteromedial to the posterior tentorial pits (fig. 55). So transparent is the cuticle of the postgenal cleft that some authors have interpreted this structure as an anterior extension of the occipital foramen. However, Crosskey (1960) has correctly interpreted the cleft as being postgenal in origin. As far as I am aware, no such modification is evident in any other Nematocera (1). Crosskey (*loc. cit.*) has likened the simuliid postgenal cleft to the condition found in certain tipulid larvae (in which the postgenae do not meet along the midline), but this is undoubtedly a non-homologous feature as judged from other characters. The postgenal cleft probably imparts a certain degree of flexibility to the head capsule, which might allow the head to withstand the forces of running water passing through the labral fan. Larvae of *Parasimulium* lack any suggestion of a postgenal cleft[10], which must be considered primitive (0) (fig. 7). The larva of *Gigantodax* (in part), and those of the fanless *Levitinia, Twinnia* and *Gymnopais,* have only a small area of slightly wrinkled cuticle in the area of the cleft. The impression given is that of a small or rudimentary postgenal cleft, if any at all. I have interpreted this latter condition as a reversal toward the primitive condition (2). The irregularity of the cuticle in the region of the cleft lends credence to this hypothesis, as no such wrinkling is evident in *Parasimulium* nor in any other Culicomorpha larva that I am aware of. In *Levitinia, Twinnia,* and *Gymnopais*, the loss of the cleft is probably related to the loss of the labral fans. However, because of the character is homoplastic within Simuliidae, the derived state can be taken only as secondary phylogenetic evidence.

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[10] I have been unable to confirm Courtney's (1986) observation of a "moderately shallow" postgenal cleft in the larva of *P. crosskeyi*.

Character 51 (p).

Lateral plate of prothoracic proleg. — A pair of apically fringed lateral plates (aflp) is situated on the prothoracic proleg of most simuliid larvae (fig. 56). The plates are immediately proximal to the apical circlet of hook, and serve to support the distal article of the proleg (Hora 1930). According to Barr (1982), they may also serve to remove the hooks of the proleg from "attachment silk". A lateral plate is present in the larva of all genera examined except *Parasimulium* (fig. 29). As no homologue of the lateral plate has been found in any other Chironomoidea, I regard the structure as a primary synapotypy of Simuliinae. The apotypic state is **1**; the plesiotypic state, which is absence of lateral plates, is **0**.

Systematics of Simuliinae

The monophyly of Simuliinae, as here defined, is very strongly supported by the 15 synapotypies given above (7 primary, 8 secondary) (fig. 5). Particularly convincing are the pupal characters, which until now have received little attention in phylogenetic reconstruction. Future work should center on structural details of the pupal gill, as our knowlege about this important character system is only rudimentary at present. The larva, too, has an array of presumed autapotypies, but additional studies will be needed before all characters can be analyzed. At present, I am unsure of how to evaluate features of the hypostoma and anal sclerite. Comparative morphological work on such structures will add immeasurably to our understanding of the early evolutionary pathways of Simuliidae.

2.8.3 Initial dichotomy of Simuliinae

2.8.3.1 Tribe **Prosimuliini** Enderlein

PROSIMULIINAE Enderlein, 1921: 199. Type genus: *Prosimulium* Roubaud, 1906.

HELLICHIINI Enderlein, 1925: 203. Type genus: *Hellichia* Enderlein, 1925.

GYMNOPAIDINAE Rubtsov, 1955: 329, 330. Type genus: *Gymnopais* Stone, 1949.

HELODONTINI[11] Ono, 1982: 280, 282. Type genus: *Helodon* Enderlein, 1921.

Diagnosis: *Male and Female:* Rs distinctly forked, forked portion conspicuously longer than its petiole; C with uniformly-sized hair-like macrotrichia only, without thickened or spiniform macrotrichia interspersed among them. Calcipala and pedisulcus absent. *Male:* ventral plate with strap-like connection between apex of anterolateral apodeme and paramere; paramere simple apically, without accessory spines. *Pupa:* Abdominal segments 4 and 5 each with large pleural plates (pleurites) laterally, these typically separated from terga and sterna of same segments by paired longitudinal bands of striate membrane (pleurite absent from segment 4 of *Levitinia*); segment 3 either without pleural membrane (the segment appearing ring-like), or membrane in the form of narrow longitudinal band. *Larva:* Antenna with proximal and medial articles unpigmented, contrasting with black distal article. Hypostoma lacking paralateral teeth. Anteromedian palatal brush of first-instar of scoop-shaped, fringed plates. Maxillary palpal sensilla of first-instar subapically situated and in linear configuration.

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[11] The spelling is here corrected from the originally published "Helodoini" (Crosskey 1985)

The tribe Prosimuliini, as here defined, comprises the following genus-group taxa: *Prosimulium s.str.*, *Helodon*, *Parahelodon*, *Distosimulium*, *Levitinia*, *Twinnia*, and *Gymnopais*. A total of 131 described species are recognized as valid at present, comprising approximately 9% of the world simuliid fauna (Crosskey 1987). The tribe is widely distributed throughout the Holarctic region, including Japan, Iceland, and the Mediterranean islands (Crosskey 1969). Representatives have been collected from as far north as Bjørnøya (Bear Island, 74°25′ N 19°00′E), to as far south as North Africa (Morocco). Prosimuliines are most frequently encountered in far northern or mountainous regions of the Holarctic. The monophyly of the tribe is supported by 5 synapotypic characters listed below.

Character 52 (p).

Pupal abdomen with large pleural plates (pleurites) on segments 4 and 5. — Pupae of *Prosimulium s.lat.*,*Twinnia*, and *Gymnopais* are unique among Simuliidae in having large pleural plates on each of abdominal segments 4 and 5 (fig. 57). The plates are so large that they are separated from the tergite and sternite by a narrow, longitudinally striated, membranous band. Segments 4 and 5 of other simuliids lack large plates, although small rounded pleurites, such as those on segments 6 - 8, are be present in some taxa (*e.g.* in some *Procnephia*, *Paracnephia*, and *"Cnephia" orientalis* Mackerras and Mackerras). This latter condition is presumed to be in the groundplan of Simuliinae (0) (see also discussion of Character 47). Presence of large pleural plates on segments 4 and 5 must therefore be derived (**1**), and can be taken as primary evidence of the common ancestory of Prosimuliini, as here defined. Abdominal segment 4 of pupal *Gymnopais* appears ring-like, the pleurite of the segment being fused to the adjacent tergite and sternite. This is interpreted as a further derived state within Prosimuliini (**2**) (see discussion of character 80 in chapter 3). Similarly, the absence of a pleurite from abdominal segment 4 of pupal *Levitinia* is interpreted as a loss (**2´**) (see discussion of character 39 in chapter 3). A summary of some of the evolutionary transformations discussed above is diagrammed in figure 17.

Character 53 (s).

Larval antenna with proximal and medial articles unpigmented, contrasting with black distal article. — Among the most distinctive features of larval Prosimuliini is color of the antenna. The proximal (p art) and medial articles (m art) are typically completely devoid of pigment, rendering the basal two-thirds of the antenna nearly transparent. This contrasts sharply with the color of the distal antennal article (d art), which is darkly pigmented (fig. 58). The only simuliid with a similarly colored antenna is the distantly related *Metacnephia*, but this is undoubtedly an independent development. No other culicomorph larva that I am aware of has the basal portion of the antenna completely unpigmented. Species of the *Prosimulium aculeatum* Rivosecchi group[12] have an irregular fuscous mottling on the basal two articles, but this is probably a secondarily derived trait, as inferred from other characters. Similarly, the pigmentation on the basal two antennal articles of *Levitinia* is probably independently derived. The apotypic state is **1**; the plesiotypic state, which is for the basal 2 articles to be pigmented, is **0**. The presumed secondary acquisition of pigmentation is indicated by **2**. Because of homoplasy, the apotypic state can be considered only a secondary phylogenetic indicator.

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[12] Some specialists recognize the genus *Urosimulium* Contini for members of this species group.

Character 54 (s).

Larval hypostoma lacking paralateral teeth. — Currie (1986) provided a review of terms used to describe the larval hypostomal teeth of Simuliidae, and suggested homologies among selected genera. The term "paralateral teeth" was proposed for the 1 - 3 additional denticulations lateral to the lateral or corner tooth. The larval hypostoma of Prosimuliini differs from that of most other Simuliidae in lacking such paralateral teeth. As a result of this arrangement, the lateral margins of the toothed portion of the hypostoma appears to be rather parallel-sided (figs. 59, 61). Absence of paralateral teeth is here considered a synapotypic feature of Prosimuliini (**1**); the plesiotypic state (**0**) is for paralateral teeth to be present. Because the derived state is a regressive feature, it can be taken only as a secondary phylogenetic indicator. A similar, but probably non-homologous, arrangement of the hypostoma is found in the larva of *Crozetia* Davies.

Character 55 (s).

Anteromedian palatal brush of first-instar larva consisting of scoop-shaped, fringed plates. — First-instar larvae of *Prosimulium s.lat., Twinnia,* and *Gymnopais* possess a series of paired, scoop-shaped, apically fringed, anteromedian palatal brushes (Craig 1974) (fig. 61, apb). Such a condition is probably synapotypic for these three taxa (**1**), although, as pointed out by Borkent and Wood (1986), the majority of simuliid genera have yet to be surveyed for this character. The presumed primitive condition is for the palatal brush to consist of small, simple hairs (**0**). Such a condition is found in first instars of *Parasimulium, Crozetia, Cnephia, Metacnephia,* and *Simulium* (Craig *loc. cit.*, Borkent and Wood *loc. cit.*). Simple hairs have also been found to comprise the anteromedian palatal brush of first-instar. *Aedes aegypti* (Linnaeus)(personal observation). The derived state can be considered only a secondary synapotypy because not enough is known about the distribution of the character at present.

Character 56 (s).

Maxillary palpal sensilla of first-instar larva subapically situated and in a linear configuration. — First-instar larvae of *Prosimulium, Twinnia* and *Gymnopais* have a unique arrangement of maxillary palpal sensilla (Craig and Borkent 1980). The sensilla are laterally situated on the palpus, and are arranged in a more or less linear fashion (**1**) (fig. 60). This contrasts with the presumed primitive condition for Nematocera, in which the sensilla of first instars are apically situated on the palpus, and arranged in a circular configuration (**0**) (Craig and Borkent *loc. cit.*) (*e.g.* fig. 30). The condition in first-instar *Parasimulium stonei* approaches that of Prosimuliini in having the sensilla laterally postioned on the palpus; however, it differs in having the sensilla arranged in the primitive circular configuration (Borkent and Wood 1986). Although this has been interpreted as an intermediate stage of a transformation series between the arrangements found in Prosimuliini and other Nematocera (Borkent and Wood *loc. cit.*), I regard the condition in *Parasimulium* as independently derived (see also discussion of character 33). Until more genera have been surveyed for this character, the derived state can be taken only as a secondary synapotypy.

Systematics of Prosimuliini

If *Prosimulium s.lat.* is really the most plesiotypic member of Simuliinae (and all available evidence points to this conclusion), then the following questions must be addressed if a satisfactory definition of Prosimuliini is to be obtained: (a) are there any other simuliids that share an immediate common ancestor with *Prosimulium*, which is not shared by any other simuliid; and (b) are there any supraspecific simuliid taxa currently included in *Prosimulium* that can be shown to be paraphyletic?

The first question has already been answered, as it is now seems well established that *Twinnia* and *Gymnopais* are derived from a *Prosimulium s.lat.* ancestor (Craig 1974, Wood 1978, Craig and Borkent 1980, Borkent and Wood 1986). Although the first-instar larva of *Levitinia* has yet to be discovered, it is clear that its members belong to a monophyletic lineage including *Twinnia* and *Gymnopais* (see chapter 3). The second question is more difficult to answer because of a lack of information about key Afrotropical forms (*viz. Procnephia* and *Paracnephia*). Crosskey (1969, 1981a) has treated such forms as subgenera of *Prosimulium* (Table 2.1); and Rubtsov (1974) has placed them, as full genera, in a "monophyletic" assemblage including *Prosimulium s.lat.* and *Gigantodax* (fig. 3, Table 2.1). However, on the basis of available information, it would appear that there is no close relationship between the African forms and *Prosimulium*. Rubtsov's inclusion of *Gigantodax* in Prosimuliini does not seem justified, as any similarities between these two groups are exclusively symplesiotypic.

Of the 5 synapotypies given in support of the monophyly of Prosimuliini, only 1 (Character 52) can be considered a primary phylogenetic indicator (fig. 5). Characters 55 and 56 seem promising as constitutive features, but require further investigation. On the whole, however, the monophyly of the tribe seems reasonably well established by the characters given above.

2.8.3.2 Tribe Simuliini Newman

SIMULIITES Newman, 1834: 387. Type genus: *Simulium* Latreille, 1802.

NEVERMANIINI Enderlein, 1921: 199. Type genus: *Nevermannia* Enderlein, 1921.

WILHELMIINI Baranov, 1926: 164. Type genus: *Wilhelmia* Enderlein, 1921.

ECTEMNIINAE Enderlein, 1930: 81. Type genus: *Ectemnia* Enderlein, 1930.

STEGOPTERNINAE Enderlein, 1930: 81. Type genus: *Stegopterna* Enderlein, 1930.

CNESIINAE Enderlein, 1934: 273. Type genus: *Cnesia* Enderlein, 1934.

FRIESIINI Enderlein, 1936: 117. Type genus: *Friesia* Enderlein, 1922. (unavailable)

ODAGMIINI Enderlein, 1936: 127. Type genus: *Odagmia* Enderlein, 1921. (unavailable)

AUSTROSIMULIINI Smart, 1945: 472. Type genus: *Austrosimulium* Tonnoir, 1925.

CNEPHIINI Grenier & Rageau, 1960: 739. Type genus: *Cnephia* Enderlein, 1921.

EUSIMULIINI Rubtsov, 1974: 256, 275. Type species: *Eusimulium* Roubaud, 1906.

Diagnosis: *Male and Female:* Rs unforked, or with obscure apical fork conspicuously shorter than its petiole; C with typical hair-like mactotrichia interspersed with thickened or spiniform macrotrichia. Calcipala typically present; pedisulcus present or absent (represented in some members as an irregularity of the cuticle). *Male:* Ventral plate with strap-like connection to paramere subapical on anterolateral apodeme (in some members represented by angular point on side of ventral plate); paramere typically with accessory spines (lacking in *Mayacnephia, Tlalocomyia* and *Cnesiamima*). *Pupa:* Abdominal segments 4 and 5 without large pleural plates (pleurites) laterally (some members with small rounded pleurites); segment 3 widely divided by pleural membrane. *Larva:* Antenna with distal article variously colored, proximal and medial articles typically pigmented (unpigmented in species of *Metacnephia*). Hypostoma with paralateral teeth. Anteromedian palatal brush of first instar consisting of simple hairs. Maxillary palpal sensilla of first instar apically situated and in circular configuration.

The tribe Simuliini comprises 18 of the 22 genera listed as valid by Crosskey (1981). In addition, I refer to the tribe two additional genera (*Procnephia* and *Paracnephia*) that have formerly been ranked as subgenera of *Prosimulium s.lat.* (Crosskey *loc. cit.*). About 1340 described species are referred to the tribe at present, which is about 90% of the total world fauna. Representatives are distributed throughout all zoogeographic regions. The monophyly of Simuliini is supported by the 5 synapotypic characters enumerated below.

Character 57 (s).

Calcipala. — The calcipala (clcp) is a flattened lobe-like projection that arises from the inner apical margin of the hind tarsomere 1 (= hind basitarsus) (fig. 62). The function of the calcipala remains unclear at present, and I am unaware of any homologue among the out-groups. No suggestion of a calcipala is evident in any member of Parasimuliinae or Prosimuliini (**0**); however, such a structure is widely and commonly distributed among members of Simuliini (**1**). The calcipala is probably a groundplan feature of Simuliini as evidenced by its presence in such primitive members as *Paracnephia,* the Australian "*Cnephia*", and the Neotropical genera formerly assigned to the tribe Prosimuliini (*cf.* Wygodzinsky and Coscarón 1973). Two of the three species assigned to the plesiotypic genus *Procnephia* have only a weakly developed calcipala, but the third, *P. rhodesianum* Crosskey, lacks one. As a weakly developed calcipala is inferred to be the groundplan condition for Simuliini, its absence in *rhodesianum* must be considered secondary. The calcipala apparently has been lost also from *Crozetia, Sulcicnephia, Metacnephia,* and certain members of *Simulium s.lat.* (**2**). Because of homoplasy, the calcipala can be considered only a secondary synapotypy. A summary of some of the transformations discussed above is illustrated in figure 22.

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Character 58 (s).

Radial sector unbranched, or with an obscure apical fork that is conspicuously shorter than its petiole. — This represents the third stage of a transformation series, that begins with the conspicuously branched radial sector of Parasimuliinae. The second or intermediate stage is exemplified by the radial sector of Prosimuliini, which has the branches more closely approximated. In its most highly derived state the radial sector is either unbranched, or is represented by an obscure apical fork. Although it might be argued that the differences between these patterns are merely a matter of degree, each state is immediately recognizable, and there has yet to be found any forms that could serve as a link between them. Therefore, it seems possible that differences in the radial sector signify a substantial phylogenetic gap between Parasimuliinae and Simuliinae on the one hand, and Prosimuliini and Simuliini on the other. The apotypic state is **1**; the plesiotypic state, which is for the radial sector to have a long, distinct fork, is **0**. State **1** is taken as a secondary synapotypy because it is a regressive feature. Evolutionary transformations of the simuliid wing are illustrated in figure 20.

Character 59 (s).

Costa with dimorphic setae. — Hackman and Väisänen (1985) concluded that a relatively simple type of costal chaetotaxy, in which slender, irregularly situated macrotrichia are the only type of seta present, is the primitive condition for Diptera (0). Such a condition occurs in the Mecoptera (*Panorpa*), nearly all the nematocerous superfamilies and many other groups of Diptera as well. Among Culicomorpha the primitive condition is evident in Dixidae, Thaumaleidae, Ceratopogonidae, Chironomidae, Parasimuliinae, and Prosimuliini. Culicidae and Chaoboridae have scale-like setae, but Hackman and Väisänen consider this to be a minor modification of the primitive condition. Similarly, the long, thin setae of Psychodidae are considered to be an independent development from the general plan. The Simuliini wing differs from those of Parasimuliinae and Prosimuliini in having a second type of seta interspersed among the characteristic hair-like macrotrichia (fig. 63). Hackman and Väisänen suggested that the presence in Simuliidae of sparsely arranged costal spinulae could be considered a synapotypy of a group of genera, but failed to elaborate. I concur with this conclusion although they examined only a limited number of genera (*Cnephia s.str.*, *Metacnephia*, *Simulium s.lat.*), and the distinction between the two types of setation is not as clear as they suggested. Primitively the differentiated seta of Simuliini appears as a somewhat thickened version of the hair-like macrotrichium (1). Such a condition is found in the Australian "*Cnephia*" (in part), *Greniera* (in part), and the male of *Procnephia*. Females of *Procnephia* lack differentiated costal setae, but it is unclear as to whether this represents the primitive condition for simuliine females, or whether it is in fact a reversal to the primitive form. Another possibility (albeit untestable at present) is that the tendency for differentiated costal setae is an underlying syapotypy for Simuliini, and the character has become variously expressed in different lineages. In its most highly derived form the differentiated seta appears as a conspicuous, blackened spinule (2). However, the distinction between the two types of setae is rather arbitrary, as an almost uninterrupted transformation series can be formed between the hair- and spine-like setae of members of Simuliini. It is possible that lineages within the tribe can be defined by the form of the costal setation, but this is an area requiring further study. Because of the instances of homoplasy indicated above, the derived state can be taken only as a secondary phylogenetic indicator. The evolutionary transformation discussed above is illustrated in figure 20.

Character 60 (s).

"Strap-like connection" between paramere and ventral plate of male arising subapically on anterolateral apodeme ("basal arm") of ventral plate. — Males of Parasimuliinae share with those of Prosimuliini a strap-like connection between the paramere and the anterolateral apodeme of the ventral plate. The strap arises from near the apex of the apodeme, and projects anterodorsally to a point where it connects with the paramere. Wood and Borkent (1982) compared this arrangement with the condition in most other simuliids, in which the paramere connects with an angular point on the side of the ventral plate. The angular point is probably the remnant of the strap-like connection, which has simply become fused to the lateral margin of the ventral plate. The anterolateral apodeme in this latter arrangement appears as a solid finger-like projection, free of any association with the paramere. An intermediate condition is evident in the male of certain genera (*e.g. Procnephia, Paracnephia, Crozetia, Mayacnephia, Cnesiamima*) which have the strap-like connection subapical on the anterolateral apodeme. I have interpreted this intermediate stage as the groundplan condition for Simuliini (**1**). The primitive condition, which is for the strap-like connection of the paramere to originate from the apex of the basal arm, is (**0**). Unfortunately, out-group comparison does not seem possible at present because I am unable to identify homologous structures among the out-groups. Character-state **1** is regarded a secondary synapotypy because it is a regressive (fusion) condition. A

summary of the hypothesized transformations is given in figure 23.

Character 61 (s).

Paramere of male with spines apically (= krameral spines). — In Simuliidae the parameres are large triangular- to subquadrate-shaped structures that arise from the anterolateral arms of the ventral plate. In many species the apical or posterior end of the paramere is armed with 1 or more "krameral spines" of various size. Typically, the spines originate directly from the apex of the paramere; although in some species, the spines appear to be isolated in the aedeagal membrane adjacent to the paramere. In certain species of *Simulium s.lat.* the paramere has along its posterodorsal margin a finger-like projection, which in turn bears a series of apical or subapical krameral spines. Presence of krameral spines, regardless of their form, is a widely and commonly encountered feature of members of Simuliini. The typical condition in Diptera is for the paramere to be simple posteriorly (*i.e.* without spines) — a feature shared by members of Parasimuliinae and Prosimuliini (**0**). Presence of krameral spines therefore must be derived, and can be taken as a synapotypy of Simuliini, as here defined. In the absence of information from the out-groups, one can only speculate about the evolutionary transformations of krameral spines within the tribe. From a developmental perspective, the presence of small spines on the apex of the paramere would be a logical first step (**1**). Such a condition is found in the following genera: *e.g. Stegopterna, Simulium s.lat.* (in part). Other conditions within Simuliini are easily derived from this hypothesized groundplan: (**1′**) development of long, stout krameral spines (*e.g. Cnesia, Gigantodax,* and *Simulium s.lat.* [in part]); (**1′′**) development of a finger-like extension on the posterodorsal margin of the paramere, on which the spines are held (*e.g. Simulium s.lat.* [in part]); and (**1′′′**) isolation of the spines in the aedeagal membrane through reduction of the apex of the paramere (*e.g. Procnephia, Paracnephia*). From this latter state, a further modified condition can be derived *viz.* loss of parameral spines (2‴) (*e.g. Mayacnephia, Tlalocomyia, Cnesiamima*). Loss of parameral spines is associated with the general reduction or loss of the paramere. It is clear that the distribution of these character-states throughout the tribe is extremely complex, and as yet not well resolved. An alternative explanation for the wide-spread occurrence of parameral spines in Simuliini is that it is actually an underlying synapotypy of the tribe, and that intra-tribal variation is the result of differential expression. But regardless of whether parameral spines prove to be a synapotypy (an evolutionary novelty present in the common ancestor of Simuliini, but with secondary modifications or losses), or is in fact an underlying syapotypy (close parallelism as a result of common inherited genetic factors), it is clear that presence of parameral spines can be considered only a secondary synapotypy of the tribe. During mating, the parameral spines are evidently erected so that they engage and push ventrally the hypogynial valves of the female sternum 8 (Davies 1965b). This widens the female cavity to facilitate insertion of the aedeagus.

Systematics of Simuliini

Simuliini is the least well-defined of the primary evolutionary lineages of Simuliidae. Of the 5 characters enumerated above, only 2 (both regressive) hold for all members of the tribe (58, 60) (fig. 5). The 3 other synapotypies (57, 59, 61) are homoplastic, the features evidently having been lost several times independently. However, no scheme of Simuliini exists (or can be constructed) in which instances of homoplasy can be completely eliminated. The most problematic species belong to *Procnephia,* which evidently comprise one of the earliest lineages of the tribe. Several of the features discussed above are only incipiently developed in that genus. Further, the group as a whole is inadequately collected, and not all character states have been firmly established. For example, the male of *P. damarensis* de Meillon and Hardy is known only from parts of dissected pupae (pharate adults), and so the apparent absence of parameral spines may in fact be the result of incomplete development.

2.9 Relationships among the primary evolutionary lineages of Simuliidae

A phylogenetic arrangement of simuliid subfamilies and tribes is diagrammed in figure 5.

The model is conservative in that it places *Parasimulium s.lat.* as the sister taxon of all other simuliids, a point on which most modern workers agree. Nevertheless, the hypothesis of a close relationship between *Parasimulium* and some other primitive-grade simuliids also deserves consideration. Enderlein (1921) was the first worker to suggest such a relationship by including *Parasimulium*, *Prosimulium*, *Cnephia* and *Helodon* in the subfamily Prosimuliinae. Stone (1963,1965) adopted a similar system by including *Parasimulium, Prosimulium, Twinnia* and *Gymnopais* in the subfamily Prosimuliinae. However, neither classification was prefaced with a discussion of characters, and their ideas have received little support over the years. More recently, Borkent and Wood (1986) provided a model in which *Crozetia* was placed as the sister taxon of the above mentioned genera (fig. 4b). This entire assemblage was held together by a single synapotypy *viz.* reduction of the labral fan in the first instar larva. While it is clear that a reduced fan is apotypic for Simuliidae (Wood 1978), there are questions about the reliability of this character as a phylogenetic indicator. First, it is a regressive feature, and thus cannot be taken as strong phylogenetic evidence. Second, the character is homoplastic within Culicomorpha. If well developed labral fans are in the groundplan of the infraorder, as suggested by Wood (1978), then they must have been lost in Chaoboridae, Thaumaleidae, Chironomidae and Ceratopogonidae. Indeed, the character is even homoplastic within Simuliidae, if it is considered that members of the *Simulium oviceps* Edwards group also have reduced fans (Craig 1977); *S. oviceps* is only remotely related to the fanless Prosimuliini. Two other characters, both features of the first-instar larva, were provided in support of the monophyly of *Parasimulium* + *Prosimulium s.lat.* + *Twinnia* + *Gymnopais* (*viz.* maxillary palpus with apical spicules; maxillary palpal sensilla subapical) (fig. 4b). Neither character has been widely surveyed in Culicomorpha, and I am therefore inclined to accept the larger suite of characters (37-51) used to support the monophyly of Simuliinae, as defined in the present work.

The initial dichotomy within Simuliinae remains somewhat more problematic. A sister-group relationship is suggested between *Prosimulium s.lat.* + *Levitinia* + *Twinnia* + *Gymnopais* (Prosimuliini), and all other Simuliinae (Simuliini). There remains still the possibility that certain primitive-grade simuliines (esp. *Procnephia, Paracnephia*) really belong to Prosimuliini, although this would assume independent evolution of several important features (characters 57-61). In the absence of complete information about the first-instar larva (in which 2 key Prosimuliini autapotypies are manifest *i.e.* characters 55 and 56), the hypothesis of a close relationship between the primitive-grade African simuliids and Simuliini is to be preferred. If the proposed definition of Simuliini is accepted, then there must have been secondary losses of the calcipala (character 57) and spiniform costal setae (character 59). However, simuliines that lack such features are referrable to the tribe based on other hypothesized synapotypies.

2.2. Matrix of characters analyzed for evidence of monophyly and suprageneric relationships of Simuliidae.

TAXON/CHARACTER	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
PARASIMULIUM s.str.	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0
ASTONEOMYIA	?	?	1'	1	1	1	1	?	?	?	?	?	?	?	0	0	0	?	?
PROSIMULIUM s.lat.	1/0	2/1/0	0	0	0	0	0	0	0/1	1'	0	0	0	1	1	1	1	1	1
LEVITINIA	0	1	0	0	0	0	0	?	0	?	0	0	0	1	1	1	1	1	1
TWINNIA	1	2	0	0	0	0	0	0	0/1	1'	0	0	0	1	1	1	1	1	1
GYMNOPAIS	1	2	0	0	0	0	0	1'	1	1'	0	0	0	0/1	1	1	1	1	1
PROCNEPHIA	0	0	0	0	0	0	0	?	0?	?	0	0	0	1	2	1	1	1	1
PARACNEPHIA	0	0	0	0	0	0	0	?		?		0	0	1	2	1	1	1	?
CROZETIA	0	0	0	0	0	0	0	?		0	0	0	0	1	2	1	1	1	1
AUSTRALIAN "CNEPHIA"	0	0	0	0	0	0	0	?		?	0	0	0	1	2	1	1	1	?
MAYACNEPHIA	0	0	0	0	0	0	0	?		?	0/1''	0	0	1	2	1	1	1	1
TLALOCOMYIA	0	0	0	0	0	0	0	?		?	0	0	0	1	2	1	1	1	1
CNESIA	0	0	0	0	0	0	0	?		?	0	0	0	1	2	1	1	1	1
GIGANTODAX	0	0	0	0	1	0	0	?		?	0	0	0	1	2	1	1	1	1
ARAUCNEPHIA	0	0	0	0	0	0	0	?		?	0	0	0	1	2	1	1	1	?
ARAUCNEPHIOIDES	0	0	0	0	0	0	0	?		?	0	0	0	1	2	1	1	1	?
CNESIAMIMA	0	0	0	0	0	0	0	?		?	?	?	?	1	2	1	1	1	?
LUTZSIMULIUM	0	0	0	0	1	0	0	?		?	1''	0	0	1	2	1	1	1	?
PARAUSTROSIMULIUM	0	1	0	0	0	0	0	?		?	0	0	0	1	2	1	1	1	1
AUSTROSIMULIUM	0	1	0	0	0	1	0	?		?	0/1''	0	0	1	2	1	1	1	1
STEGOPTERNA	0	0	0	0	0	0	0			0	1	0	0	1	2	1	1	1	1
GRENIERA	0	0	0	0	0	0	0	?		?	1''	0	0	1	2	1	1	1	1
ECTEMNIA	0	0	0	0	0	0	0	?		?	1''	0	0	1	2	1	1	1	1
CNEPHIA	0	0	0	0	0	0	0	1'		0	0	0	0	1	2	1	1	1	1
METACNEPHIA	0	0	0	0	0	0	0	0		0	0	0	0	1	2	1	1	1	1
SIMULIUM s.lat.	0	1/0/1'	0	0	1	1	0/1	0		0	0/1''	0	0	1	2	1	1	1	1

TAXON/CHARACTER	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61
PARASIMULIUM s.str.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ASTONEOMYIA	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0
PROSIMULIUM s.lat.	1	1	1	1	1	1	1	1	1	1	1/2	1	1	1	0	0	0	0	0
LEVITINIA	1	1	1	1	1	1	1	2	1	2'	2	1	?	?	0	0	0	0	0
TWINNIA	1	1	1	2	1	2	1	2	1	1	1	1	1	1	0	0	0	0	0
GYMNOPAIS	1	1	1	2	1	2	1	2	1	2	1	1	1	1	0	0	0	0	0
PROCNEPHIA	1	1	1	1	1	1	1	1	?	0	0	0	?	?	1/2	1	1	1	1'''
PARACNEPHIA	?	1	1	1	1	1	1	1	1	0	0	0	?	?	1	1	2	1	1'''
CROZETIA	1	1	1	2'	1	2	1	1	1	0	0	0	0	0	2	1	2	1	0?
AUSTRALIAN "CNEPHIA"	?	1	1	1	1	1	1	1	1	0	0	0	0	?	1	1	0,1,2	1	0/1
MAYACNEPHIA	1	1	1	1	1	1	1	1	1	0	0	0	?	?	1	1	2	1	2'''
TLALOCOMYIA	1	1	1	1	1	2	1	1	0	0	0	0	?	?	1	1	2	1	2'''
CNESIA	1	1	1	1	1	1	1	1	1	0	0	0	?	?	1	1	2	1	1'
GIGANTODAX	1	1	1	1	1	1	1	1/2	0	0	0	0	0	0	1	1	2	1	1'
ARAUCNEPHIA	?	1	1	1	1	1	1	1	0	0	0	0	?	?	1	1	2	1	1
ARAUCNEPHIOIDES	?	1	1	1	1	1	1	1	1	0	0	0	?	?	1	1	2	1	1
CNESIAMIMA	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	2	1	2'''
LUTZSIMULIUM	?	?	?	1	1	1	1	1	1	0	0	0	?	?	1	1	2	1	2'''
PARAUSTROSIMULIUM	1	1	1	1	1	1	1	1	0	0	0	0	?	?	1	1	2	1	1
AUSTROSIMULIUM	1	1	1	1	1	2'	1	1	0	0	0	0	?	?	1	1	2	1	1
STEGOPTERNA	1	1	1	1	1	1	1	1	1	0	0	0	?	0	1	1	1/2	1	1
GRENIERA	1	1	1	0	2	1	1	1	0	0	0	0	?	?	1	1	2	1	1
ECTEMNIA	1	1	1	1	1	1	1	1	0	0	0	0	?	?	1	1	2	1	1
CNEPHIA	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	1	2	1	1
METACNEPHIA	1	1'	1	1	1	1	1	1	1	0	1	0	0	0	1/2	1	2	1	1
SIMULIUM s.lat.	1	1'	1	1	1	1/2'	1	1/2	0	0	0	0	0	0	1/2	1	2	1	1-1''

2.10 Zoogeographic Considerations

Little can be inferred about the geographical history of Simuliidae. The family is represented only sporadically in the fossil record, and the earliest known inclusions (early Cretaceous) lack features that permit placement beyond level of tribe. Further, adult black flies have tremendous dispersal capabilities, as inferred from the occurrence of simuliids (*Crozetia crozetensis* (Womersley)) on such remote oceanic islands as the subantarctic Iles Crozet (47°S, 51°E). This volcanic archipelago is more than 3000 km southeast of the southern tip of Africa, which is where the next closest population of black flies occurs. Such dispersal abilities might obscure patterns attributable to vicariance. Nevertheless, the present-day distribution of the primary lineages is interesting, and warrants consideration.

The first question that must be addressed is when Simuliidae originated. Recent work by Jell and Duncan (1986) shows that several families of Culicomorpha were already well differentiated by early Cretaceous times: Dixidae, Chaoboridae (Chironomapterinae), Simuliidae, and Chironomidae (Tanypodinae); hence, it is clear that the origin of the infraorder was much earlier than this. Of particular interest is when the various lineages of Chironomoidea separated. The oldest fossils definitely referable to the superfamily, which are members of the so called "Architendipedidae" Rodendorf (*Architendipes tshernovskyi* Rodendorf, *Palaeotendipes alexii* Rodendorf), are of Upper Triassic age (Hennig 1981). If these fossils really belong to the stem group of Chironomidae, as suggested by Hennig, and if Simuliidae is really the sister taxon of Chironomidae + Ceratopogonidae (fig. 1), then Simuliidae also must have been in existence during Upper Triassic times. Indeed, the same argument can be used to set a minimum age for Culicoidea and Thaumaleidae. Further discoveries are needed to determine the approximate ages of the various families.

The following discussion of the geographical history of Simuliidae is based on several assumptions. First, it is assumed that the family originated during Upper Triassic times (or at a time when there was only a single continental land mass — Pangea). But even if the family originated later than this, say during middle or late Jurassic times, then the origin of Simuliidae would still be effectively Pangean, because gaps between the separating continents would pose only a minimal barrier to dispersal. Second, it is assumed that habitat requirements for Simuliidae have remained constant over time. The primitive habitat for Simuliidae is presumed to be mountainous (a fact corroborated by the large number of plesiotypic forms presently associated with that habitat). This is consistent with the conclusion of Brundin (1966) that Chironomidae must also have taken its origin in cool mountain streams. When it is considered that the distribution of Thaumaleidae also follows that of mountains, it would seem that such a habitat is a groundplan feature of Chironomoidea as a whole. If the earliest lineages of Simuliidae were indeed restricted to mountainous terrain (and all available evidence points to this conclusion), then colonization of a particular region can be correlated with orogenic events (*i.e.* primitive simuliids could not have occupied an area until after mountains had lifted). The third assumption is that some of the present-day patterns are attributable to vicariance, and are not merely the result of dispersal. While it is acknowledged that instances of long distance dispersal have occurred (*Crozetia*), it is also clear that presumably habitable areas have remain uncolonized (*e.g.* the Hawaiian and Falkland Islands).

The primary lineages of Simuliidae are distributed as follows presently: (1) Parasimuliinae — Western Nearctic; (2) Prosimuliini — Holarctic; and (3) Simuliini — Cosmopolitan. The geographic distributions of Parasimuliinae and Prosimuliini, and those of the most plesiotypic members of Simuliini, are shown in figure 24. What follows is an interpretation about how these patterns arose. The timing and sequence of major geological events (plate movements) is taken from Hallam (1981) and Smith *et al.* (1981).

Members of Parasimuliinae are presently restricted to the southwestern Nearctic

Region. More specifically, they are known only from the Coastal and Cascade Ranges of the western United States. Assuming that Parasimuliinae had a Pangean origin, or originated at a time when gaps between the continents were narrow, then their present day distribution can be described only as relict, meaning that their distribution is considerably reduced over what it once must have been. Indeed, geological evidence suggests that Parasimuliinae could not have occupied their present range until the early Eocene, as this is when the oldest formations in which they now live (the Coastal Range) first began to lift (Baldwin 1981). The origin of the Cascade Range is even more recent, arising during Plio-Pliestocene times. It is impossible to determine what has caused the extirpation of Parasimuliinae over most if its range, or when the reduction took place. Perhaps modern-day representatives of the subfamily survived by invading a unique larval habitat, the hypogean zone.

Prosimuliini members are presently restricted to the Holarctic region. One explanation for this distribution is that the tribe originated in Laurasia, and has subsequently failed to colonize the southern continents. The oldest known fossil attributable to Simuliinae is of lower Cretaceous age, which means that Prosimuliini may have differentiated at a time when the Tethys Sea separated Laurasia and Gondwanaland. This gap, although narrow in the western Mediterranean, persisted from the Middle Jurassic through the Cretaceous; however, it is doubtful that such a narrow gap would pose a serious barrier to dispersal. Perhaps the absence of Prosimuliini from the Afrotropical and Oriental regions is related to other kinds of barriers, or because of a lack of suitable habitat. As already indicated, prosimuliines typically inhabit mountainous or high latitude areas. The Sahara desert presently serves as a barrier between Morocco (the southern limit of Prosimuliini) and the mountains of western Africa, but may also have served as a barrier during earlier times. Tropical forests once covered the Sahara, and the flat terrain of the region would have proven uninhabitable for Prosimuliini. Similarly, the Gobi desert of

Mongolia, and the Talimupendi desert of northern China, form an effective barrier between the Pamir + Tian Shan + Altai + Sayan mountains to the north (where prosimuliines occur), and the eastern Himalaya and Kunlunshanmai mountains in the south (where they are apparently absent). The apparent absence of Prosimuliini from the western Himalaya is anomalous, as there are no apparent barriers between those mountains and the Pamirs. Whether this is due to some unknown dispersal barrier, or is merely a collecting artifact, cannot be determined at present. The absence of Prosimuliini from most of the Middle East, and from much of central Europe and Asia, can be attributed to a lack of suitable habitat (*i.e.* lack of running water; absence of mountainous terrain).

In the New World, prosimuliines evidently range only as far south as California. I am not aware of any records from Mexico, including the mountainous regions of Baja California. As in the Old World, the most significant barriers to southward dispersal appear to be deserts, or at least semi-arid flatlands. The Mojave and Sonoran deserts form an effective present-day barrier between the Sierra Nevadas of California, and the Sierra Madre Occidental of Mexico; farther east, the Rio Grande valley poses a barrier between the Rocky Mountains and the Sierra Madre Oriental. The regional shift to a drier climate began only during the early Eocene (Axelrod 1979); but the earlier presence of tropic savanna and dry tropic forest, and lack of mountainous terrain, would also have provided a barrier.

Most present day barriers for Prosimuliini are not of a distance that would preclude long distance dispersal. Further, some of the barriers have appeared only recently. This suggests that the tribe might have originated at more northerly latitude, and that they have diversified (at least in the southern part of the range) relatively recently.

Another possible explanation for the strictly Holarctic occurrence of Prosimuliini is extinction. Perhaps the tribe was once distributed over a much broader area, but has subsequently become extirpated in the southern hemisphere. One can speculate on the possible causes of extinction (climatic changes? competition?), but such hypotheses can be corroborated only through discovery of extralimital fossils.

Members of the tribe Simuliini are distributed over all continental land masses except Antarctica, and so little can be inferred about their historical zoogeography if the tribe is considered as a whole. Focus is therefore centered on the most primitive members. My criteria of "primitiveness" is as follows: (1) forms in which the calcipala is weakly developed; (2) forms in which the radial sector has an obscure apical fork, or in which the suggestion of a fork is given by the appearance of two rows of setae near the apex; (3) forms in which the differentiated costal setae are merely thickend versions of the hair-like macrotrichium (*i.e.* not spiniform); (4) forms in which the connection between the paramere and ventral plate is manifestly strap-like (*i.e.* not in the form of an angular point on the lateral margin of the ventral plate); and (5), forms in which the parameral spines are in the form of minute denticles. All of these features belong to the presumed groundplan of Simuliini, and represent the earliest stages of development of key Simuliini synapotypies.

The criteria of "primitiveness", as outlined above, can be taken only as a general guide, as instances of homoplasy (especially reversals) are not uncommon among Simuliini (see discussion of Simuliini groundplan apotypies). Consequently, features that seem plesiotypic on *prima facie* evidence may actually be apotypic reversals to the primitive condition. Examples of this would be the absence of a calcipala in species of *Metacnephia*; and the lack of spiniform costal setae in certain species of *Greniera*. However, there are other simuliines in which most or all of the criteria are satisfied. These I would refer to the earliest lineages of the tribe: *Procnephia, Paracnephia,* the Australian "*Cnephia*", *Crozetia,* and *Mayacnephia.*

If it is accepted that these genera are really the most plesiotypic members of Simuliini, then it seems significant that they are distributed predominantly in the southern hemisphere (fig. 24). *Procnephia* and *Paracnephia* are restricted to the southern part of Africa; the Australian "*Cnephia*" (as the name suggests) occur on continental Australia, as well as on Tasmania; *Crozetia* occurs only on the remote, subantarctic, Iles Crozet; and *Mayacnephia* is distributed chiefly in central America (although several species range into the Rocky Mountains of North America). Mention should also be made of the Neotropical "Prosimuliini" *sensu* Wygodzinsky and Coscarón, which are distributed throughout the South American Andes. The occurrence of *Mayacnephia* in Central and North America not withstanding, the overall distribution of Simuliini is suggestive of a Gondwanaland origin.

Simuliini is by far the most successful of the primary lineages of black flies, both in terms of species diversity, and overall distribution. The success of the tribe may be attributed in part to the ability of its members to move out of the mountains. Having done so, the immature stages were able to inhabit the vast array of running-water habitats present in other physiographic regions.

Summary of the geographical history of the primary lineages of Simuliidae

(1) Simuliidae is hypothesized to have originated during Upper Triassic times. Evidence is taken from the fossil record of related Chironomoidea ("Architendipedidae"), and from the hypothesized relationships of simuliids to other families. On this basis, Simuliidae is presumed to have had a Pangean (or effectively Pangean) origin.

(2) The distribution of Parasimuliinae is relict, although it is noted that present-day representatives of the subfamily could not have occupied their range until the early Eocene at the earliest.

(3) Prosimuliini and Simuliini had already separated by early Cretaceous times.

(4) It is postulated that the Holarctic distribution of Prosimuliini is the result of a Laurasian origin. The fact that relatively narrow present-day barriers separate prosimuliines from the southern hemisphere is suggestive of a more northerly origin for the tribe, and that diversification may not have occurred until relatively recently. Possibly Prosimuliini once had a much broader distribution, and has subsequently become expirpated from the southern part of its range.

(5) The prevalence of primitive-grade Simuliini in the southern hemisphere (esp. Southern Africa and Australia) is suggestive of a Gondwanaland origin. The success of the tribe is attributed to the ability of its members to move out of the mountains.

2.11 DISCUSSION

As indicated from the outset, the distribution of apotypic character states among simuliids is complex, owing largely to the intricate network of reversals or parallelisms that must have occurred during differentiation of the earliest lineages. This, plus incomplete knowlege about all life-history stages of black flies, has frustrated efforts to resolve phylogenetic relationships.

Early taxonomic works concentrated mainly on description of species, with relatively few supraspecific taxa being recognized. It was not until the middle of the twentieth century that enough was known about the world fauna to stimulate serious phylogenetic thought. Most present-day notions about simuliid relationships originated during the fifties and sixties, when the debate about the fanless condition sparked a number of important works. The seventies saw a decline in the number of phylogenetic treatments, although application of phylogenetic techniques *sensu* Hennig contributed toward the testability of hypotheses. Discovery of females and larvae of *Parasimulium* in the early eighties has rekindled interest in the origin of Simuliidae, but has resulted in conflicting hypotheses depending on whether adult (Wood and Borkent 1981) or larval (Borkent and Wood 1986) characters are considered paramount. Cytology has also played an important role in unraveling simuliid relationships; but in the absence of information about *Parasimulium* and other key taxa, and in recognizing the limitations of the technique in determining the direction of evolution, it will remain to the systematist to provide a detailed reconstructed phylogeny.

It is generally agreed that the most primitive simuliids belong to the following taxa: *Parasimulium, Prosimulium s.lat., Twinnia, Gymnopais, Crozetia, Procnephia,* and

Paracnephia. Understanding the relationships of these taxa is central to determining the primary lineages of the family. Historically, three main questions have been asked: (1) what is the relationship of *Parasimulium* to other black flies?; (2) what is the polarity of the fanless condition in black fly larvae?; and (3) what are the tribal limits of Prosimuliini and Simuliini? These questions must be considered individually.

Results of the present study indicate a sister-group relationship between *Parasimulium* and all other black flies, thus supporting the hypothesis of Wood and Borkent (1981). Rejected is the hypothesis of a close relationship between *Parasimulium* and some typical members of the Prosimuliini *sensu* Crosskey, as suggested by characters of the first-instar larva (Borkent and Wood 1986). The primary character used in support of this latter hypothesis (loss of the labral fan) is regressive and subject to homoplasy. The status of *Parasimulium (Astoneomyia)* remains uncertain, although current evidence suggests that it belongs to a monophyletic group including *Parasimulium s.str*. Wood and Borkent (1981) have suggested that *Astoneomyia* alone may be the sister taxon of all other simuliids, based on features of the male genitalia. Discovery of the larva and immature stages of *A. melanderi* remains a priority.

Discovery of fully fanned larvae of *Parasimulium* corroborates the hypothesis of Wood (1978) that absence of fans is a secondary or derived feature of black flies, and brings into question the special status given to *Gymnopais* and *Twinnia* (Gymnopaiidinae) by some specialists. If we are to assume, as does Rubtsov (1956, 1974), that the fanless condition is primitive for Simuliidae, and we accept the hypothesis of a sister-group relationship between *Parasimulium* and all other black flies (as even Rubtsov would have it, *cf.* fig. 3a)), we would then have to assume that the simuliid labral fan has evolved at least twice — once in *Parasimulium,* and once in all other black flies. This would be extremely unparsimonious, given the unlikelihood of such a complex structure evolving on more than one occasion. Results of the present study support the conclusion of Wood

(1978) that *Gymnopais* and *Twinnia* are probably derived from a *Prosimulium s.lat.* ancestor.

The third question is somewhat more difficult to answer. Wygodzinsky and Coscarón (1973) asserted that there was no clear-cut separation between Prosimuliini and Simuliini, at least as understood by workers of the day. Further, they maintained that most definitions of Prosimuliini were based on symplesiotypic characters, and could not be upheld in a cladistic system. Crosskey (1969, 1981a) admitted that "no hard and fast line can be drawn between the two tribes...", although it was not his intention to construct a system based on strict phylogenetic relationships. Rather, Crosskey (1981) attempted to arrive at a convenient division within Simuliinae "which undoubtedly reflects some kind of phyletic cleavage between the 'prosimuliines' (typically forms without spiniform vestiture on the wing veins, often with forked radial sector, with feeble mesepisternal [katepisternal] sulcus, without a hind-leg pedisulcus, often with strong pupal abdominal sclerites and tail-hooks, and usually with very ill-formed cocoon), and the 'simuliines' (typically forms with spiniform as well as hair-like vein vesture, with unforked radial sector, with well-formed mesepisternal [katepisternal] sulcus, with undifferentiated pupal abdominal sclerites and no definite tail-hooks, and usually with a discretely-formed cocoon)". There are two problems with Crosskey's definition of Prosimuliini. First, as correctly indicated by Wygodzinsky and Coscarón (1973), the definitive characters are all plesiotypic, and cannot by used to show relationships. Second, many of the taxa that Crosskey refers to Prosimuliini are not defined by tribal characters. Following is a list of "prosimuliine" genera that do not fit the characterizations given above:

(1) Genera with well-developed spiniform vestiture on veins: *Procnephia, Crozetia, Mayacnephia, Tlalocomyia, Cnesia, Gigantodax, Araucnephia, Araucnephioides, Cnesiamima, Lutzsimulium, Paraustrosimulium* , *Sulcicnephia, Stegopterna, Greniera* (in part), *Ectemnia, Cnephia,*

Metacnephia.

(2) Genera without a fork in the radial sector: *Procnephia, Paracnephia, Crozetia, Mayacnephia* (in part), *Tlalocomyia, Cnesia, Gigantodax, Araucnephia, Auraucnephioides, Cnesiamima, Lutzsimulium, Paraustrosimulium, Sulcicnephia, Metacnephia* (in part), *Stegopterna.* The following genera have only a obscure apical fork: *Mayacnephia* (in part), *Greniera, Ectemnia, Cnephia, Metacnephia* (in part).

(3) Genus with a well-developed katepisternal sulcus: *Paraustrosimulium.*

(4) Genera with a deep pedisulcus on second tarsomere of hind leg: *Sulcinephia* (several other genera have members in which a shallow pedisulcus is present; and there are others that have a distinct wrinkling of the cuticle in the area of the pedisulcus).

(5) Genera without strong pupal abdominal sclerites: *Greniera, Metacnephia, Sulcicnephia* [?].

(6) Genera without strong pupal tail-hooks (terminal spines): *Gymnopais* (in part), *Tlalocomyia, Paraustrosimulium, Metacnephia, Sulcicnephia.*

(7) Genera with a discretely formed pupal cocoon: *Ectemnia, Metacnephia, Sulcicnephia.*

Although convenient in that approximately equal numbers of species are in each of the two tribes, the criteria by which a genus is relegate to one or the other is strictly subjective, and some features do not hold for the majority of included genera (*e.g.* characters of the wing veins). For example, Crosskey (1969) originally referred *Metacnephia* to the tribe Simuliini because "The balance of characters in *Metacnephia* taken together make it best to assign the genus to Simuliini...". Later, in his 1981 classification, Crosskey relegated the same genus to Prosimuliini, but provided no specific reasons for that action. If overall "balance of characters" is taken into consideration (*i.e.* without regard to whether character states are primitive or derived), then it is clear that the placement of not only *Metacnephia* is equivocal, but other genera as well. For example, *Sulicnephia* fails to satisfy 6 of the 7 criteria used to define Prosimuliini, but is nonetheless relegated to that tribe. One can assume only that the one concordant feature, a feeble katepisternal sulcus, was considered more important than all the others combined. But if this were so, why wasn't *Paraustrosimulium*, which has a well developed katepisternal sulcus, referred to Simuliini?

Crosskey (1987) maintains that "classifications are needed for practical ends (taxa definition, identification) but phylogenies are not essential for day to day purposes." The implication is that "convenient" but paraphyletic groupings should be maintained over a system based on phylogenetic relationships. I cannot agree — at least with respect to the higher classification of the family. First, a system based on phylogenetic relationships need not be inconvenient to the non-taxonomist. Indeed, if the limits suggested in the present work are accepted, then all taxa in all life-history stages (excluding egg) can be placed unequivocally at the tribal level. The only "inconvenience" is that there is a greater proportion of simuliines to prosimuliines, the proportion being approximately 12 : 1 (in Crosskey's system the proportion is about 5 : 1). However, rejection of tribal limits based on disproportionality would be inconsistent with the acceptance of Parasimuliinae, which has less that one percent of the entire world simuliid fauna. Virtually all modern workers have accepted this subfamily. Would changing the suprageneric classification of Simuliidae be disruptive to the non-taxonomist? Not necessarily. By far the majority of non-systematic work on the family is centered on *Simulium s.lat.*, which remains within Simuliini. The other genera consist of relatively few species, and few of these are of medical and veterinary importance. Anyway, only seldom is there reference to suprageneric categories in non-taxonomic works.

Whether a classification be based on purely phenetic grounds or phylogenetic relationships should not be determined solely with respect to simuliidology . Consideration should be given also to the taxonomic state-of-affairs in other Diptera, and in particular Culicomorpha. Led by the pioneering work of Hennig, dipterists have turned increasingly to phylogenetic systematics to resolve relationships. Nowhere is this more evident than in Chironomidae, which has received a number of important phylogenetic treatments in recent years (*e.g.* Brundin 1966, 1983; Borkent 1984; Sæther 1976, 1977, 1979a, 1979b, 1983; Brundin and Sæther 1978). Phylogenetic works have also appeared on Ceratopogonidae (*e.g.* Remm 1975, Grogan and Wirth 1979, Borkent and Forster 1986), Dixidae (Disney 1983), and Chaoboridae (Sæther 1970, Borkent 1979). Important contributions on Simuliidae have been produced already by Wood (1978), Wood and Borkent (1981) and Borkent and Wood (1986), and it is hoped that the trend will continue if systematic work on black flies is to keep pace with that on other Diptera.

One important advantage of Crosskey's system relates to formal ranking of taxa. Two systems are widely used: one, as advocated by Rubtsov (1974), recognizes many small genera (59) but no subgenera; the other, which is favored by Crosskey (1981a, 1987), recognizes fewer genera (23), of which the largest are divided into a number of subgenera. Because of the large number of genera recognized in Rubtsov's system, a larger number of suprageneric taxa are needed to accommodate them. For example, a total of 4 subfamilies and 5 tribes are recognized in Rubtsov's (1974) classification. Crosskey's system is much simpler, recognizing only 2 subfamilies and 2 tribes. Simuliidae is a relatively small family of Diptera, and has far fewer species than several other culicomorph families (Table 2.3). Given the structural homogeneity of black flies, the large number of suprageneric taxa advocated by Rubtsov hardly seems justified, especially when compared with the classifications of other more speciose families (Table 2.3). Accordingly, fewer genera should be recognized. This would make the classification less cumbersome for the non-specialist.

Unlike Crosskey, Rubtsov (1974) favors a classification based on phylogenetic relationships. Unfortunately, characters were analyzed under the assumption that simuliids were derived from a chironomid ancestor, which has resulted in a number of serious errors about character-state polarity (*e.g.* the interpretation that the fanless condition is primitive for Simuliidae). Although Rubtsov provided a section on the "taxonomic characteristics of simuliids and the direction of their evolution", nowhere is it indicated how the characters are nested in the concluding dendrogram (figs. 3a, 3b). Thus, I am unable to determine what synapotypies, if any, were used to define his suprageneric taxa. Let us consider the subfamily "Prosimuliinae" (*Prosimulium s.lat., Procnephia, Paracnephia, Gigantodax*). If we are to accept that *Procnephia, Paracnephia,* and *Gigatodax* all belong to a monophyletic group including *Prosimulium s.lat.*, then characters 57 - 61 (all presumed Simuliini synapotypies) must either have been independently derived in the first 3 mentioned genera, or were lost (as reversals) in members of *Prosimulium s.lat.* Neither option seems very parsimonious. In the absence of any clearly stated synapotypies for Prosimuliinae *sensu* Rubtsov, the hypothesis of a close relationship between *Prosimulium* and the above-mentioned genera is rejected. Similar problems are evident with other of Rubtsov's taxa as well. The only subfamily that is undoubtedly monophyletic is Parasimuliinae.

In summary the suprageneric classification advocated in the present work, based on phylogenetic relationships, bridges the gap between between the two most widely used schemes. The advantage of this system is that it reflects accurately relationships among the earliest lineages of Simuliidae, and permits unequivocal placement of genera at the tribal level. Moreover, it proves the basis from which to interpret the zoogeographic and evolutionary history of the family. Such endeavors have proven difficult in the past,

Table 2.3. Comparison of supraspecific classifications of selected families of Culicomorpha, relative to numbers of species.

	Rubtzov 1974	Crosskey 1987	Knight & Stone 1977 Knight & Stone 1978	Wirth *et al.* 1974	Ashe 1983* Coffman & Ferrington 1984†
FAMILY	Simuliidae	Simuliidae	Culicidae	Ceratopogonidae	Chironomidae
SUBFAMILIES	4	2	3	4	10*
TRIBES	5	2	10	7	24*
GENERA	59	23	34	63	326*
SPECIES	1,000+	1,461	3,071	3,870	10,000 - 15,000†

because of lack of fundamental knowledge about even the most basic relationships.

Another advantage of the system proposed here is that it is testable. Hypotheses of relationship can be corroborated or falsified based on additional information. The pioneering work of Wood and Borkent provided the cladistic framework on which the present study is based. It is hoped that hypotheses suggested here will also be tested, and will be corroborated or falsified on the basis of their own merits (*i.e.* on the basis of the characters used). Accordingly, the classification based on this system should be accepted or modified as additional information comes available. This will lead eventually to a well-corroborated and widely accepted classificatory system, which will lead ultimately to stability.

Figure 1. Dendrogram showing phylogeny of Culicomorpha, as discussed in text.

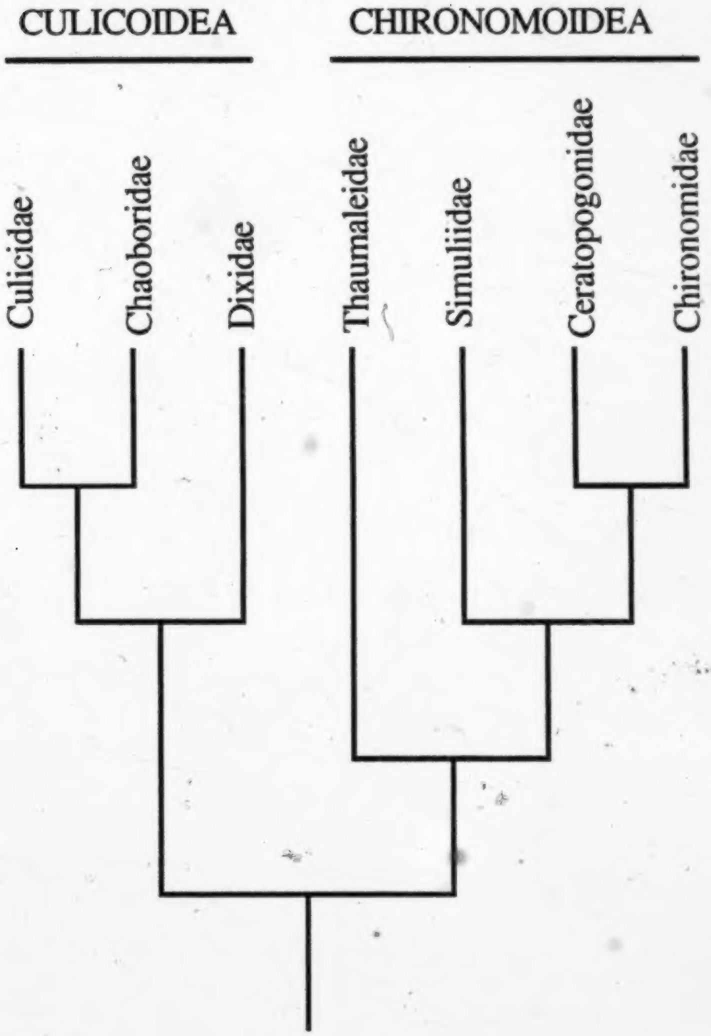

CULICOIDEA
CHIRONOMOIDEA
Culicidae
Chaoboridae
Dixidae
Thaumaleidae
Simuliidae
Ceratopogonidae
Chironomidae

Figure 2. Diagrammatic representation of spiracular systems of larval Culicomorpha: diagrams at internodes indicate the presumed groundplan for a clade; black segment = larval head.

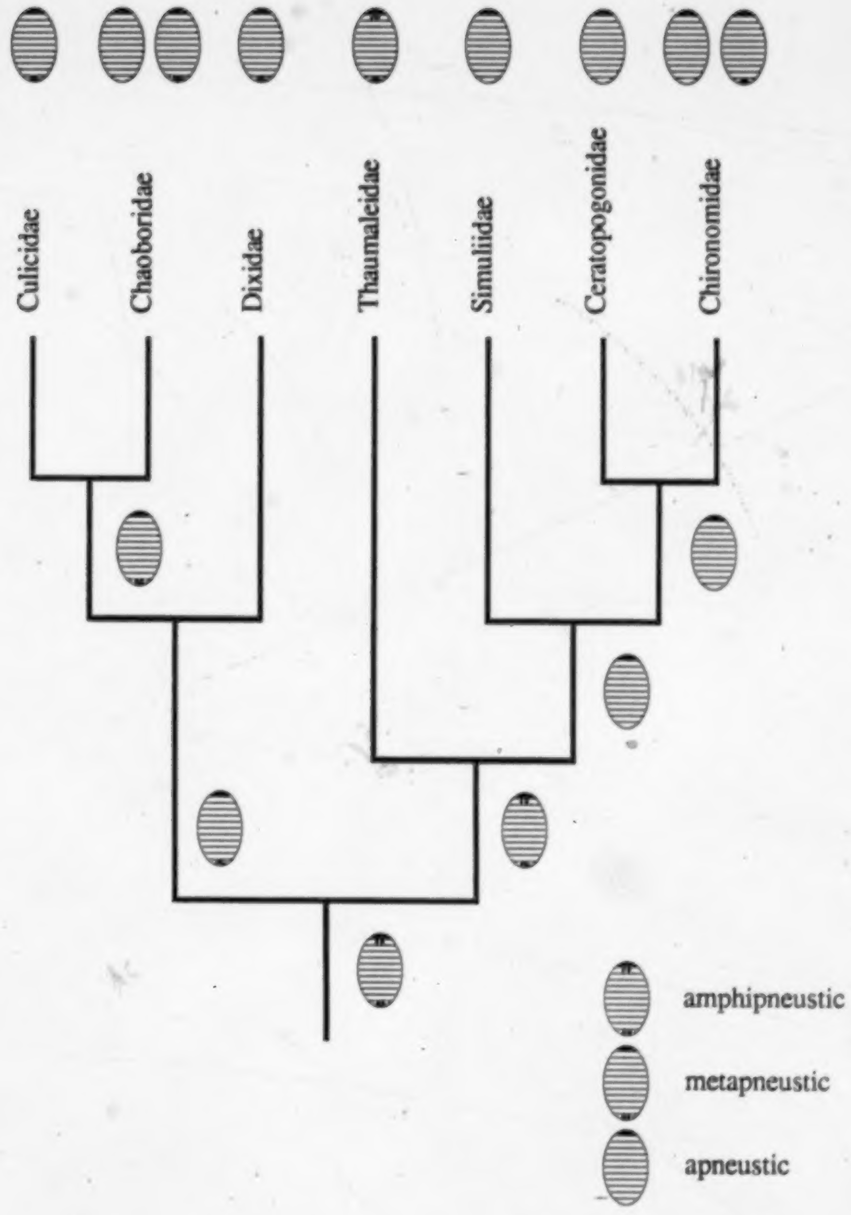
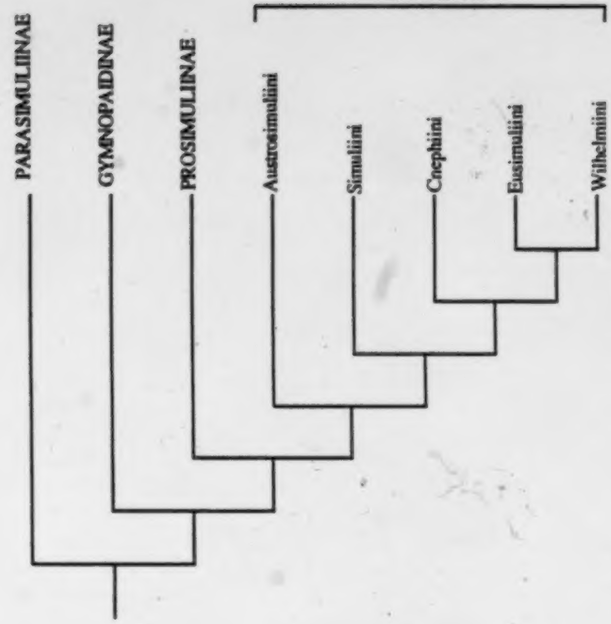
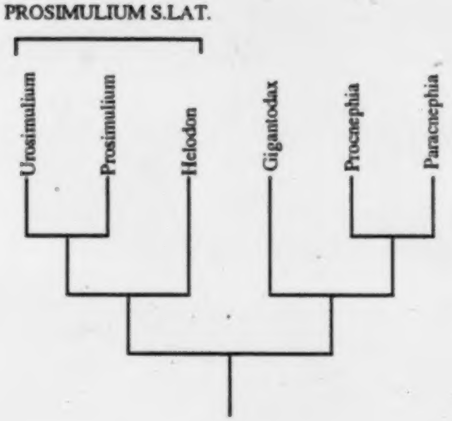

Culicidae
Chaoboridae
Dixidae
Thaumaleidae
Simuliidae
Ceratopogonidae
Chironomidae
amphipneustic
metapneustic
apneustic

Figure 3. Rubtsov's (1974) interpretation of relationships among Simuliidae. **A.** Dendrogram showing hypothesized relationships of suprageneric taxa of Simuliidae. **B.** Dendrogram showing hypothesized relationships of genera of Prosimuliinae.

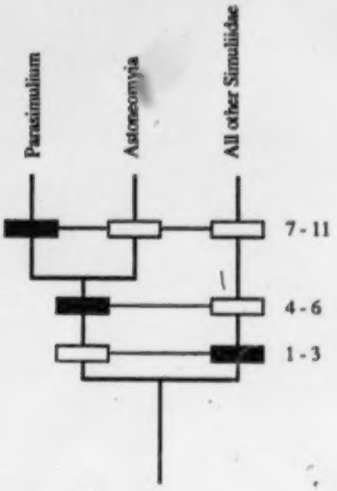

SIMULIINAE
PARASIMULIINAE
GYMNOPAIDINAE
PROSIMULIINAE
Austrosimuliini
Simuliini
Cnephiini
Eusimuliini
Wilhelmiini

A

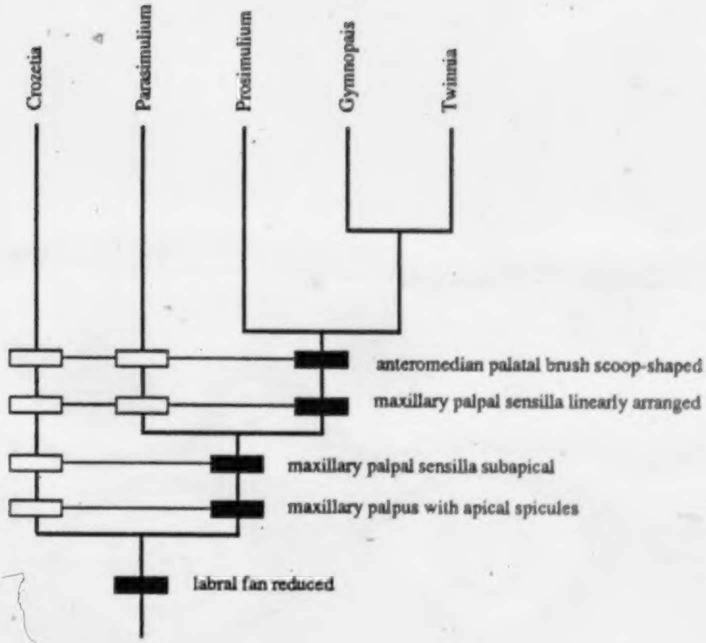

PROSIMULIUM S.LAT.
Urosimulium
Prosimulium
Helodon
Gigantodax
Procnephia
Paracnephia

B

Figure 4. **A**. Relationship of *Parasimulium* to other Simuliidae, as suggested by features of the adult (Wood and Borkent 1982): (1) large upper facets and small lower facets of male eye distinctly separated by a line of discontinuity; (2) branches of radial sector (R_{2+3} and R_{4+5}) closely approximated; (3) sternum X of female divided medially; (4) Katepisternum greatly reduced, almost pointed ventrally in profile; (5) mesepimeral tuft lost; (6) peglike seta at apex of gonostylus lost; (7) supra-alar notch narrow and deep, with sharp supra-alar crest and narrow lateral opening (8) gonocoxite with apicolateral finger-like extension and row of setae along adjacent edge; (9) ventral plate with forked apex, the apicolateral prongs immobilized by "inner gonostylus"; (10) median sclerite long and strap-like, with apically widened portion; (11) gonostylus with subapical cusp on dorsal side. **B**. Relationship of *Parasimulium* to some Prosimuliini (*sensu* Crosskey), as suggested by features of the first instar larva (Borkent and Wood 1986): synapotypies are indicated directly on the cladogram.


Parasimulium
Astoneomyia
All other Simuliidae
7 - 11
4 - 6
1 - 3

A


Crozetia
Parasimulium
Prosimulium
Gymnopais
Twinnia
anteromedian palatal brush scoop-shaped
maxillary palpal sensilla linearly arranged
maxillary palpal sensilla subapical
maxillary palpus with apical spicules
labral fan reduced

B

Figure 5. Cladogram showing hypothesized relationships of primary evolutionary lineages of Simuliidae: (24) stemmatic bulla; (25) flagellum of 8 articles; (26) katepisternum reduced; (27) mesepimeral tuft lost; (28) basal medial cell lost; (29) basal radial cell reduced; (30) gonostylus with apical peglike seta lost; (31) mating behaviour; (32) autogenous females; (33) maxillary palpus of first-instar larva with subapically arranged sensilla; (34) abdominal segment 8 of larva with a single, large, midventral tubercle; (35) hypogean habitat of immatures; (36) lack of pigmentation of immatures; (37) eye of male with line of discontinuity between large upper facets and small lower facets; (38) radial sector with branches (R_{2+3} and R_{4+5}) closely approximated; (39) false vein (m-cu fold) forked apically; (40) katepisternal sulcus (mesepisternal groove); (41) sternum X of female divided medially; (42) plastron network covering the entire respiratory organ; (43) felt chamber of respiratory organ lost; (44) pupal spiracle communicating with "lumen" of plastron; (45) pupal sternites 6 and 7 (at least) divided medially by a semi-membranous longitudinal striate area; (46) pupal abdominal segments 3 - 8 with terga and sterna divided by pleural membrane; (47) pleuron of pupal abdominal segments 6 and 7 (at least) with recurved hooks and plates (pleurites); (48) pupal abdominal tergites 5 or 6 - 9 each with an anterior row of posteriorly-directed spines; (49) larval antenna of three articles; (50) larval headcapsule with postgenal cleft; (51) prothoracic proleg of larva with lateral plate; (52) pupal abdomen with large pleural plates on abdominal segments 4 and 5; (53) larval antenna with proximal and medial articles unpigmented, contrasting with black distal article; (54) larval hypostoma lacking paralateral teeth; (55) anteromedian palatal brush of first-instar larva consisting of scoop-shaped, fringed plates; (56) maxillary palpal sensilla of first-instar larva subapically situated and in a linear configuration; (57) calcipala on inner apical margin of hind basitarsus; (58) radial sector unbranced, or with an obscure apical fork that is conspicuously shorter than its petiole; (59) costa with differentiated setae; (60) vental plate of male with "strap-like connection" to paramere arising subapically on anterolateral apodeme ("basal arm"); (61) paramere of male with spines or hooks apically.

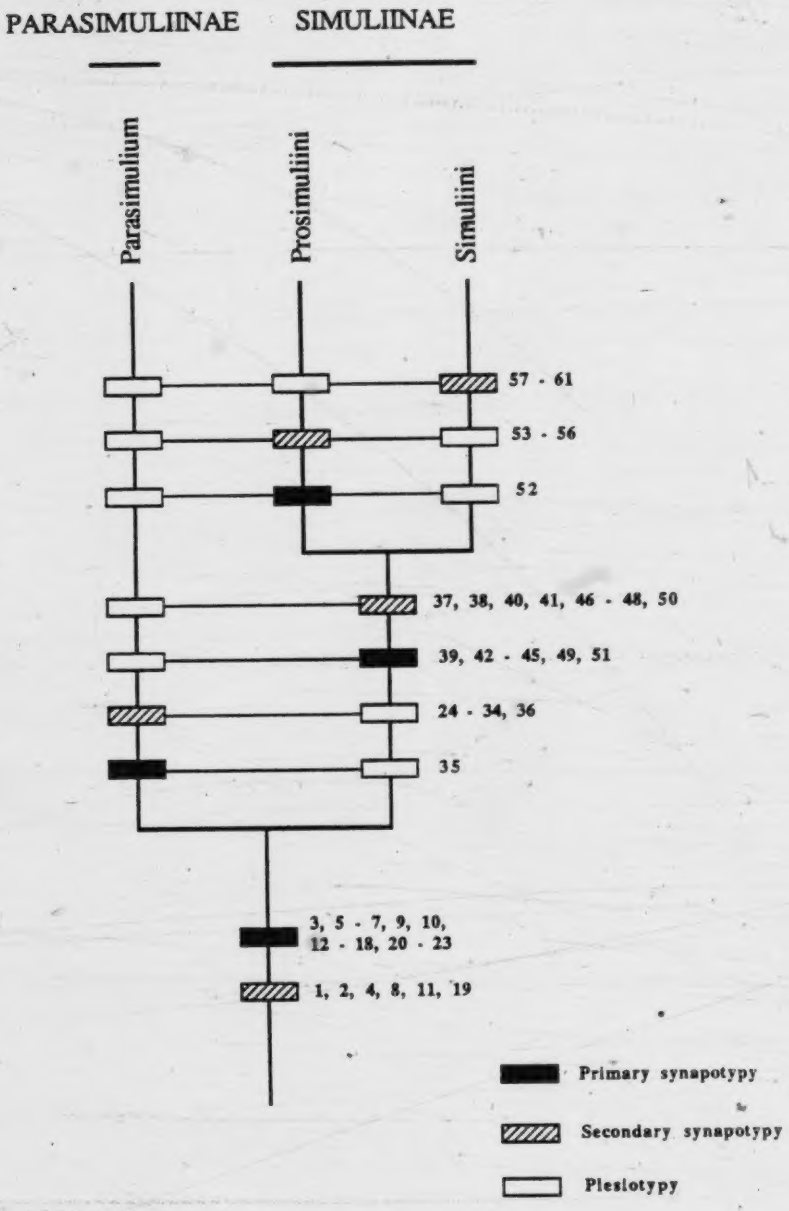
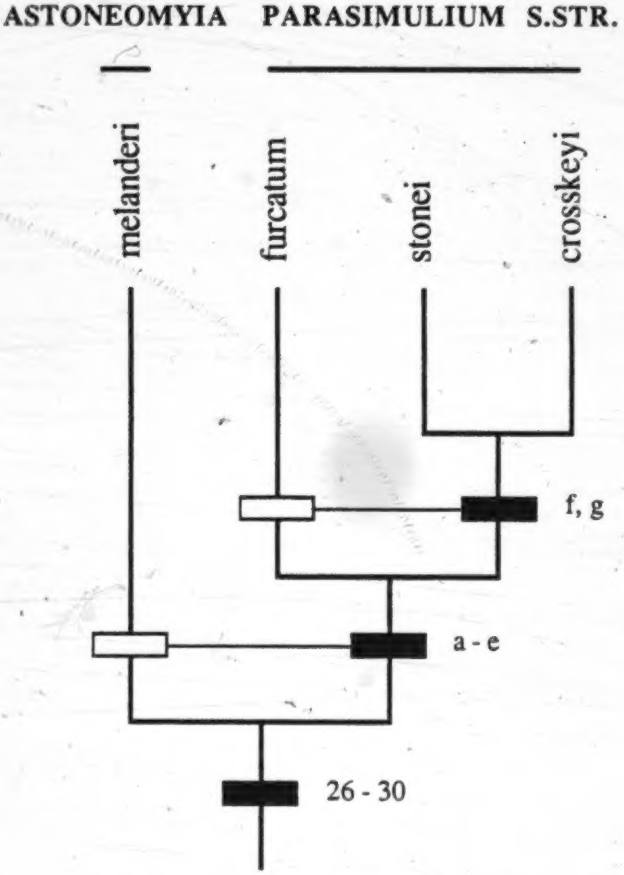
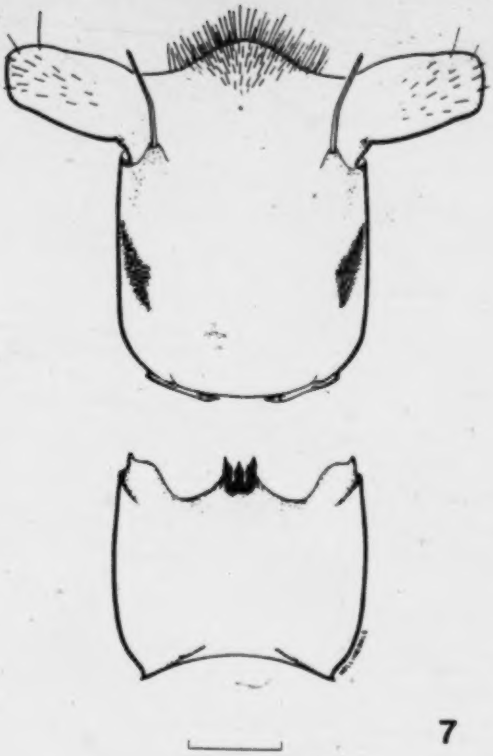

PARASIMULIINAE
SIMULIINAE
Parasimulium
Prosimuliini
Simuliini
57 - 61
53 - 56
52
37, 38, 40, 41, 46 - 48, 50
39, 42 - 45, 49, 51
24 - 34, 36
35
3, 5 - 7, 9, 10, 12 - 18, 20 - 23
1, 2, 4, 8, 11, 19
Primary synapotypy
Secondary synapotypy
Plesiotypy

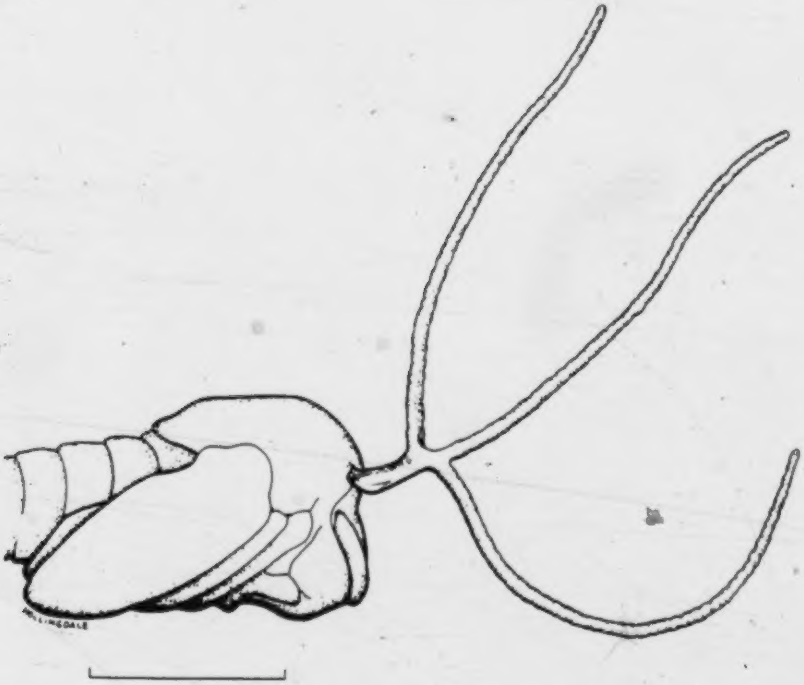
Figure 6. Cladogram showing hypothesized relationships of species of *Parasimulium*; only those characters confirmed for both *Parasimulium s.str.* and *Astoneomyia* are given as synapotypies of the genus: (26) Katepisternum reduced; (27) Mesepimeral tuft lost; (28) Basal medial cell lost; (29) Basal radial cell reduced; (30) Gonostylus with apical peglike seta lost; (a) supra-alar notch narrow and deep; (b) gonocoxite with apicolateral finger-like extension; (c) median sclerite long and strap-like, with apically widened portion; (e) gonostylus with subapical cusp ("inner gonostylus") on dorsal side; (f) scape yellow; (g) tergites 1 and 2, and sternites 1 - 3, yellow.


ASTONEOMYIA
PARASIMULIUM S.STR.
melanderi
furcatum
stonei
crosskeyi
f, g
a - e
26 - 30

Figures 7 - 8. *Parasimulium crosskeyi* Peterson: (7) larval head capsule (upper, dorsal view; lower, ventral view), scale = 0.25 mm; (8) pupal thorax and respiratory organ (lateral), scale = 1.0 mm.



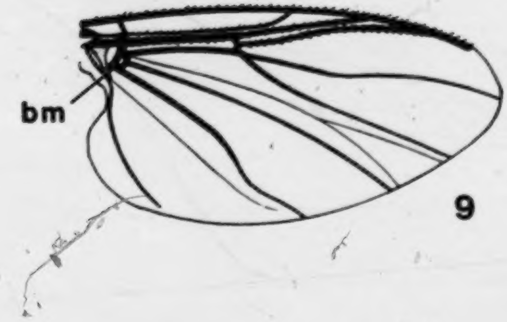
7



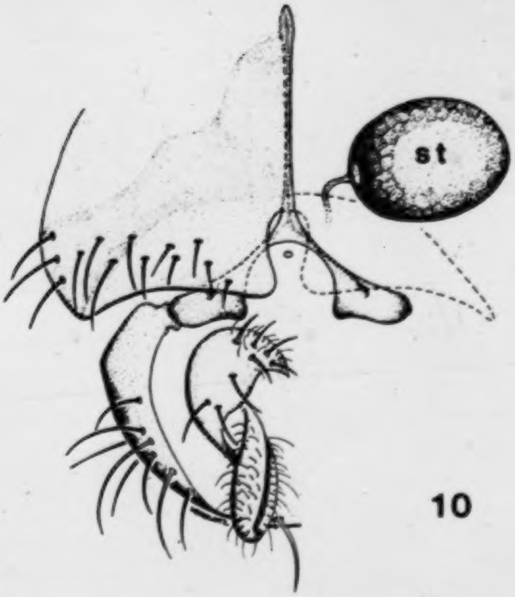
8

Figures 9 -14. Selected apotypies of the family Simuliidae, as discussed in text: (9) wing of *Mayacnephia* sp. (dorsal); (10) terminalia of female of *Simulium nebulosum* Currie and Adler (ventral view with hypogynial valve, sternum X, and cercus removed on left side); (11) pupa of *Mayacnephia* sp. (lateral), scale = 1.0 mm; (12) larva of *Simulium pugetense* (Dyar and Shannon) (lateral); (13) terminal abdominal segments of larva of *Simulium venustum* Say (dorsal); (14) prothoracic proleg of larva of *Prosimulium travisi* Sommerman (lateral).

Abbreviations: ap = anal papillae; as = anal sclerite; bf = basal fenestra; bm = basal medial cell; lf = labral fan; pp = posterior proleg; ro = respiratory organ; st = spermatheca; tp thoracic proleg.



9



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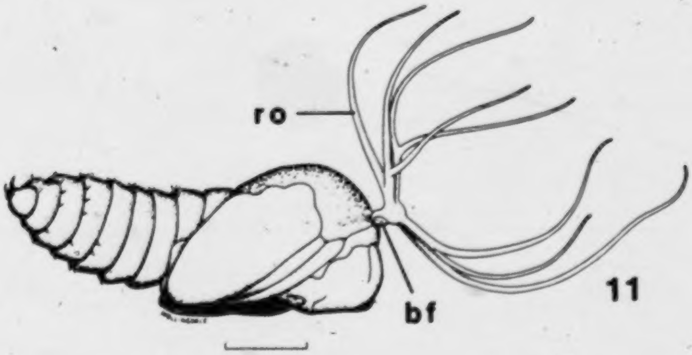
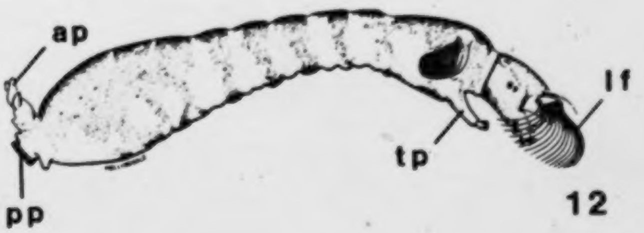
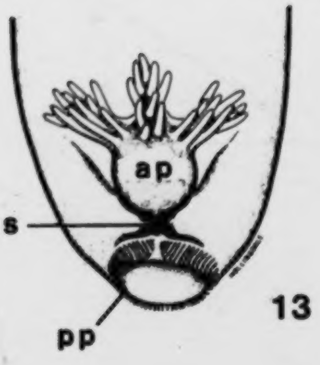


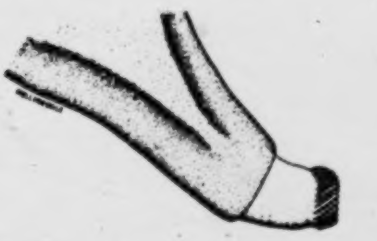
11



12



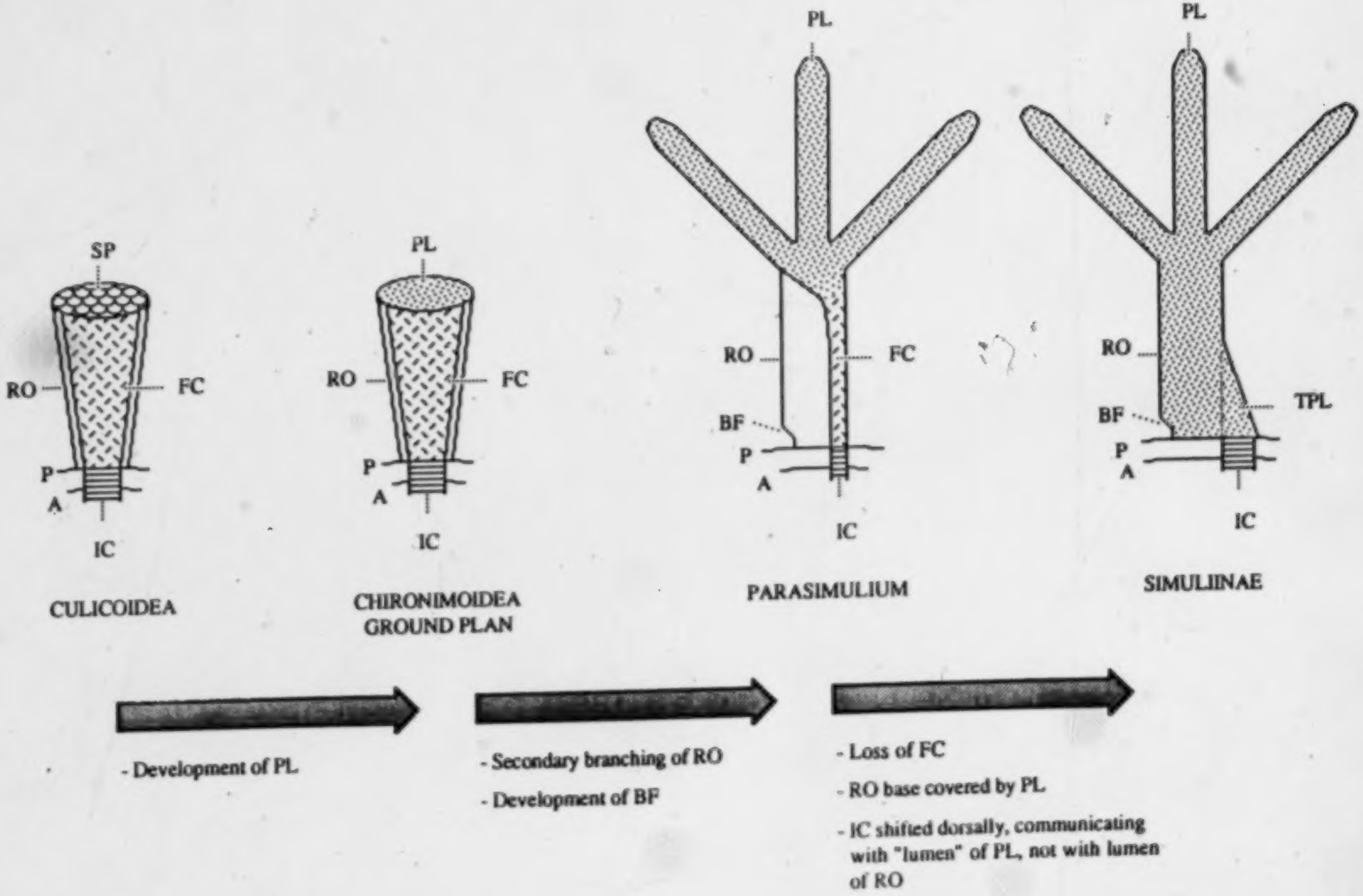
13



14

Figure 15. Hypothesized transformations of the pupal respiratory organ of selected Culicomorpha, as discussed in text.

Abbreviations: A = pharate adult cuticle, BF = basal fenestra, FC = felt chamber, IC = intercuticular tracheal connection, P = pupal cuticle, PL = plastron, RO = respiratory organ, SP = sieve plate, TPL = thickened part of plastron.


SP
RO
FC
P
A
IC
CULICOIDEA
PL
RO
FC
P
A
IC
CHIRONIMOIDEA
GROUND PLAN
PL
RO
FC
BF
P
A
IC
PARASIMULIUM
PL
RO
BF
TPL
P
A
IC
SIMULIINAE

- Development of PL

- Secondary branching of RO
- Development of BF

- Loss of FC
- RO base covered by PL
- IC shifted dorsally, communicating with "lumen" of PL, not with lumen of RO

Figure 16. Structural differences between the pupal respiratory organ of *Parasimulium*, and that of all other Simuliidae: (i) cross section through branch of respiratory organ; (ii) cross section through base of respiratory organ.

Abbreviations: A = pharate adult cuticle, FC = felt chamber, LRO = lumen of respiratory organ, MWRO = main wall of respiratory organ, P = pupal cuticle, PL = plastron, SPO = spiracular opening, TPL = thickened part of plastron.

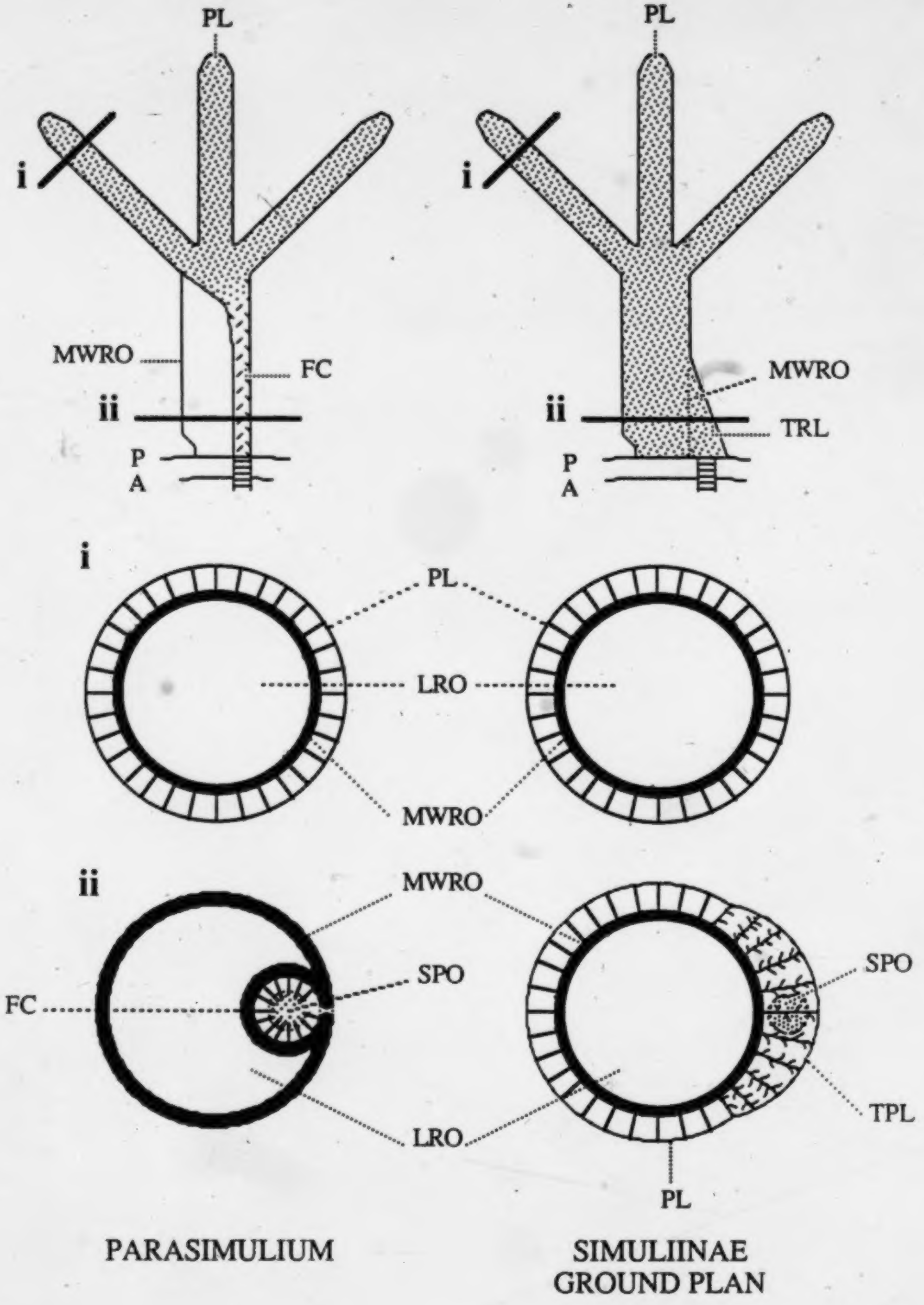

PL
i
MWRO
FC
ii
P
A
PL
i
MWRO
ii
TRL
P
A
i
PL
LRO
MWRO
ii
MWRO
SPO
FC
LRO
SPO
TPL
PL
PARASIMULIUM
SIMULIINAE
GROUND PLAN

Figure 17. Hypothesized transformations of the simuliid pupal pleuron, as discussed in text.

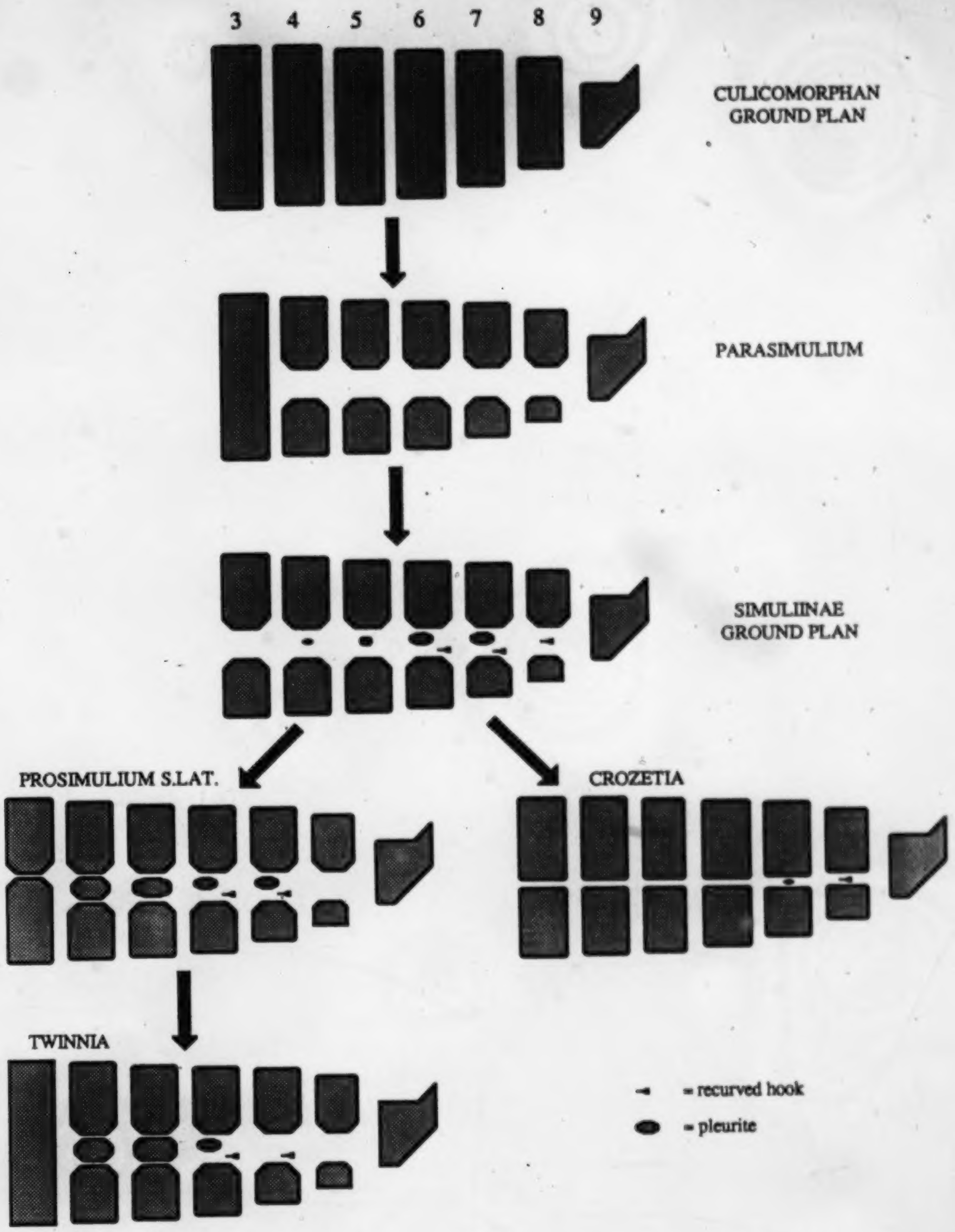

3
4
5
6
7
8
9
CULICOMORPHAN GROUND PLAN
PARASIMULIUM
SIMULIINAE GROUND PLAN
PROSIMULIUM S.LAT.
CROZETIA
TWINNIA
= recurved hook
= pleurite

Figure 18. Hypothesized transformations of the simuliid pupal tergum, as discussed in text.

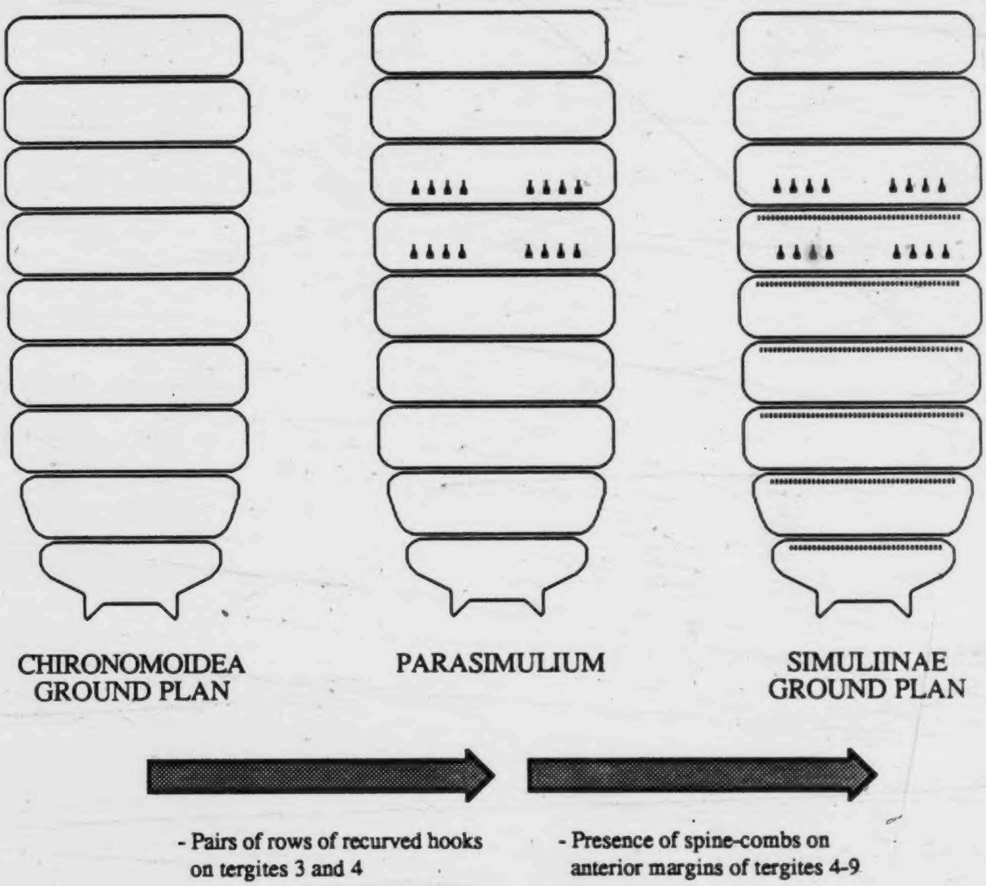

CHIRONOMOIDEA GROUND PLAN
PARASIMULIUM
SIMULIINAE GROUND PLAN
- Pairs of rows of recurved hooks on tergites 3 and 4
- Presence of spine-combs on anterior margins of tergites 4-9

Figure 19. Hypothesized transformations of the simuliid pupal sternum, as discussed in text.

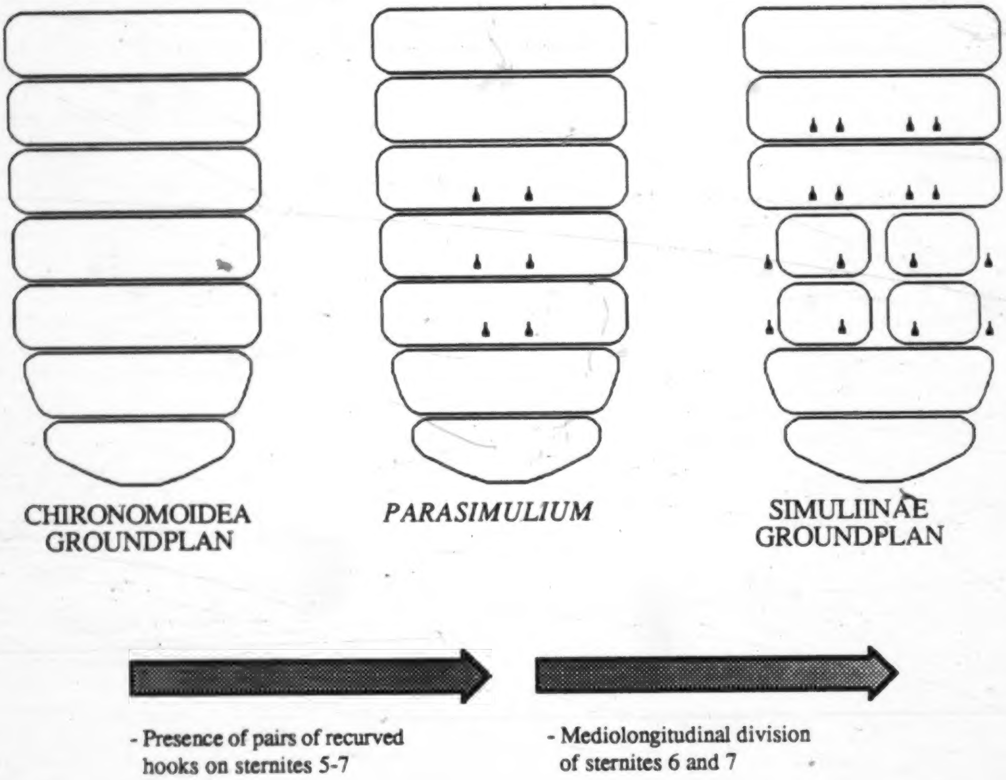

CHIRONOMOIDEA GROUNDPLAN
PARASIMULIUM
SIMULIINAE GROUNDPLAN
- Presence of pairs of recurved hooks on sternites 5-7
- Mediolongitudinal division of sternites 6 and 7

Figure 20. Hypothesized transformations of the simuliid wing, as discussed in text (dorsal views of right wing): (28) basal medial cell lost; (29) basal radial cell reduced in length; (38) radial sector with branches (R_{2+3} and R_{4+5}) closely approximated; (39) false vein (m-cu fold) forked apically; (58) radial sector unbranced, or with an obscure apical fork that is conspicuously shorter than its petiole; (59) costa with differentiated setae.

Abbreviations: A_1, A_2 = branches of anal veins; br = basal radial cell; C = costa; CuA_1, CuA_2 = anterior branches of cubitus; f vn = false vein (m-cu fold); M_1, M_2 = posterior (sectoral) branches of media; R_1 = anterior branch of radius; R_2, R_3, R_4, R_5 = posterior (sectoral) branches of radius; Sc = subcosta.

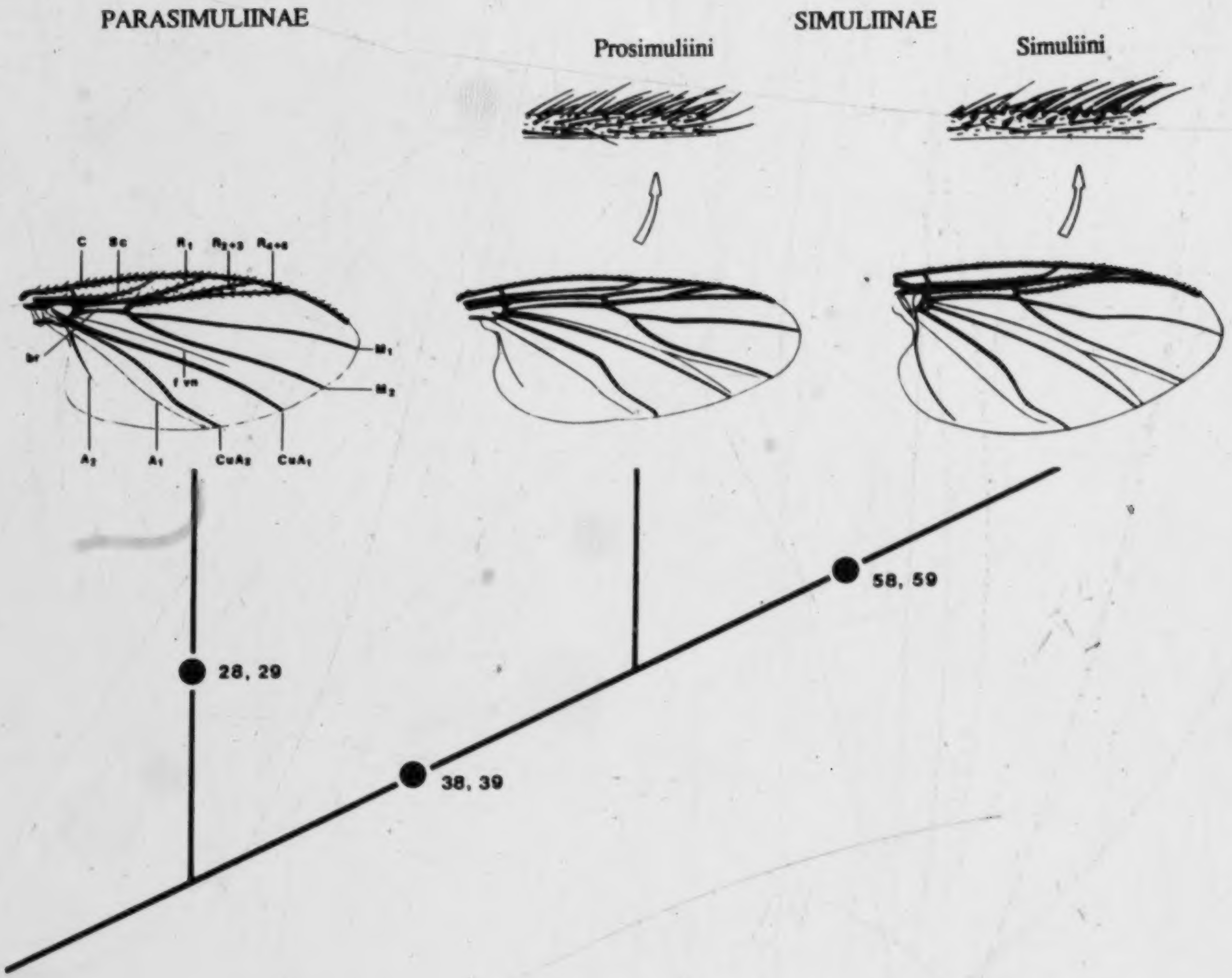

PARASIMULIINAE
SIMULIINAE
Prosimuliini
Simuliini
C
Sc
R1
R2+3
R4+5
br
f vn
M1
M2
A2
A1
CuA2
CuA1
28, 29
38, 39
58, 59

Figure 21. Hypothesized transformations of female sternum X, as discussed in text (ventral view; diagrammatic): darkly stippled area = sternum X; lightly stippled area = cercus.

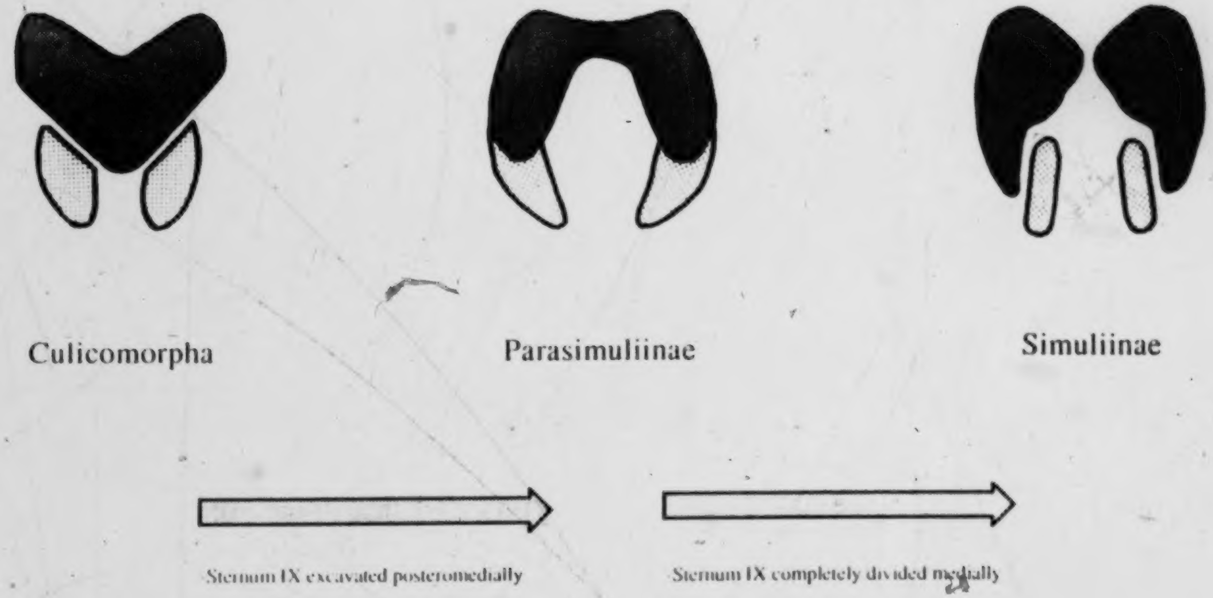
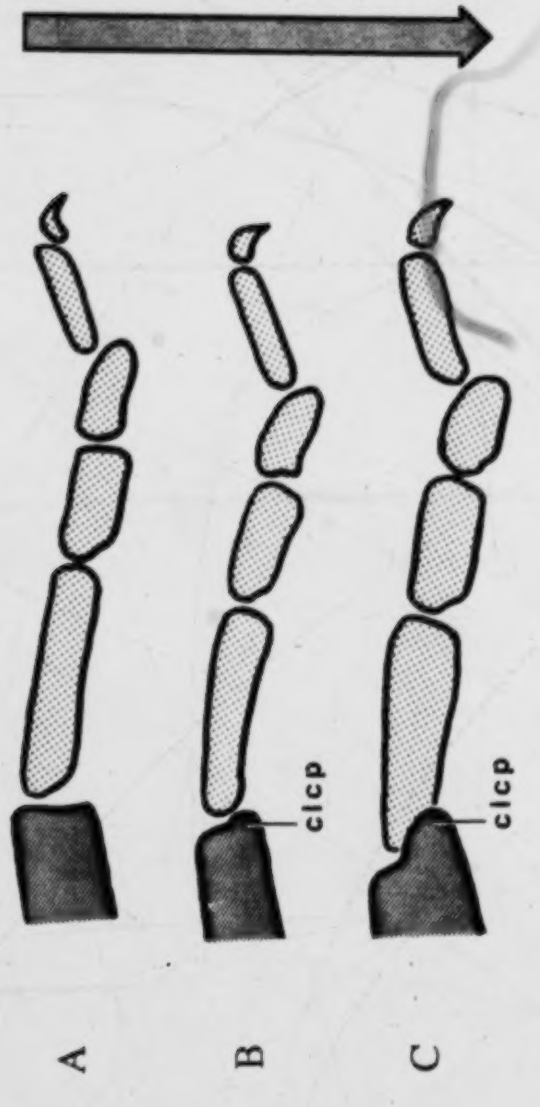

Culicomorpha
Parasimuliinae
Simuliinae
Sternum IX excavated posteromedially
Sternum IX completely divided medially

Figure 22. Hypothesized transformations of the simuliid hind tarsomere 1 (hind basitarsus) (ventral view, diagrammatic): (**A**) condition as found in Parasimuliinae and Prosimuliini; (**B**) presumed ground-plan condition for Simuliini, (**C**) ultimate development of calcipala, as found in *Stegopterna* spp. Darkly stippled area = hind tarsomere 1 (apical portion only); arrow indicates direction of evolution.

Abbreviation: clcp = calcipala


A
B
C
clcp
clcp

6

Figure 23. Hypothesized transformations of the terminalia of male Simuliidae, as discussed in text (lateral view of right side; diagrammatic): (60) strap-like connection between paramere and ventral plate arising subapically on anterolateral apodeme (basal arm); (61) paramere with setae or spines apically.

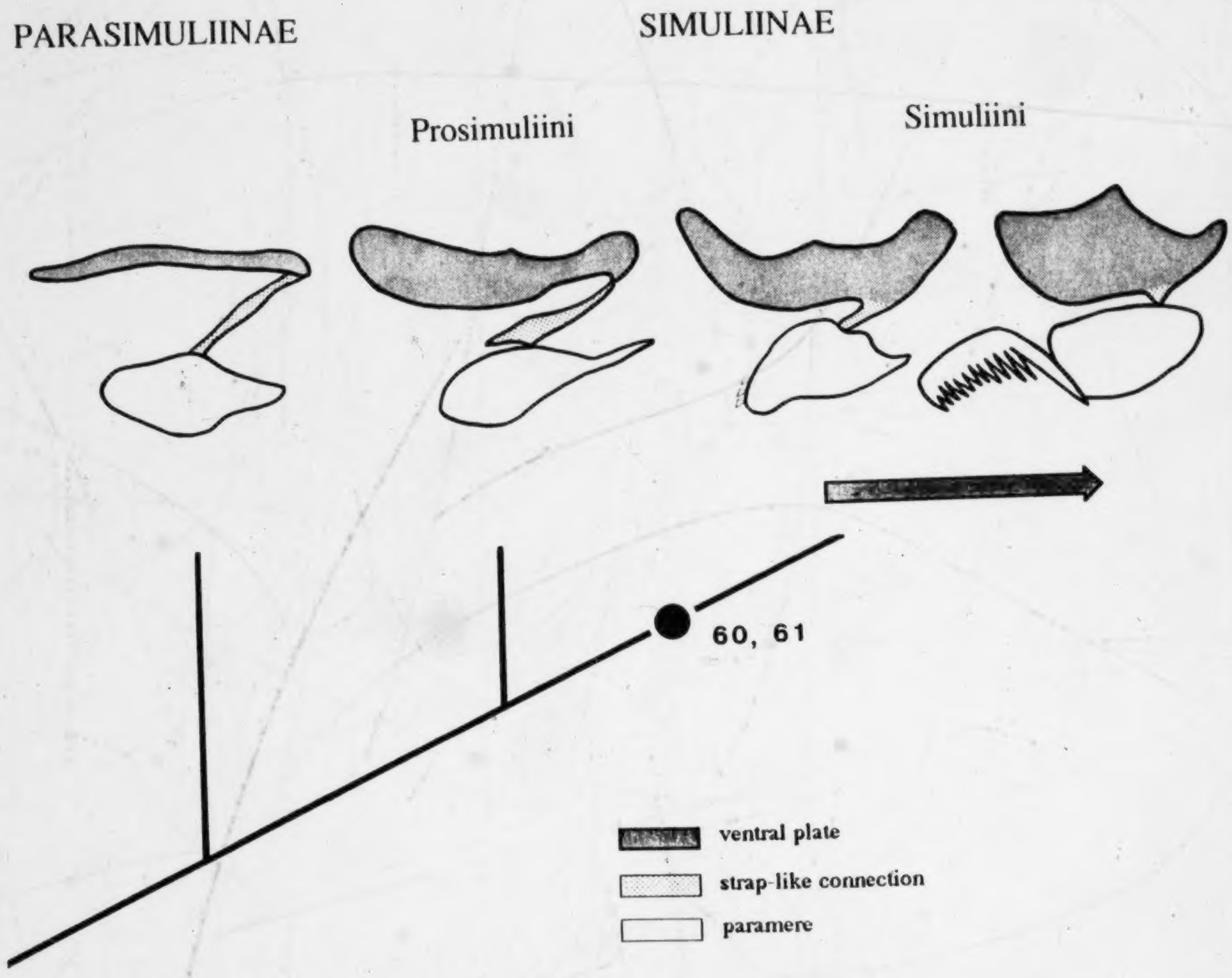
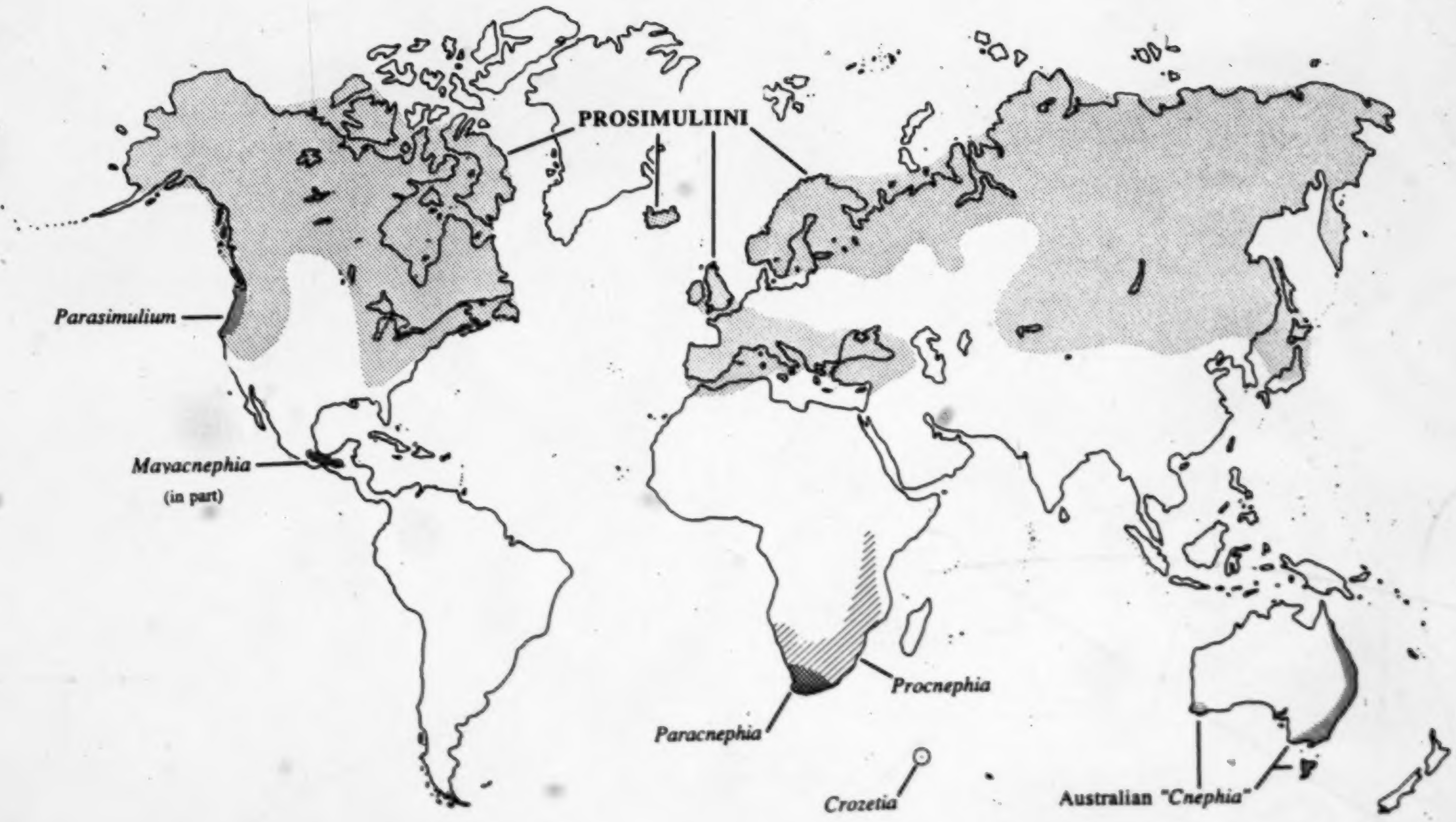
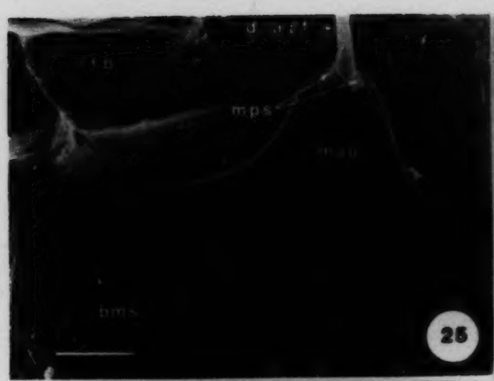

PARASIMULIINAE
SIMULIINAE
Prosimuliini
Simuliini
60, 61
▨ ventral plate
▨ strap-like connection
☐ paramere

Figure 24. Present-day distribution of Parasimuliinae (*Parasimulium* Malloch *s.lat.*), Prosimuliini, and some plesiotypic members of Simuliini (*Procnephia* Crosskey, *Paracnephia* Rubtsov, *Crozetia* Davies, the Australian "*Cnepha*", and *Mayacnephia* Wygodzinsky and Coscarón (in part)).


PROSIMULIINI
Parasimulium
Mavacnephia
(in part)
Paracnephia
Procnephia
Crozetia
Australian "Cnephia"

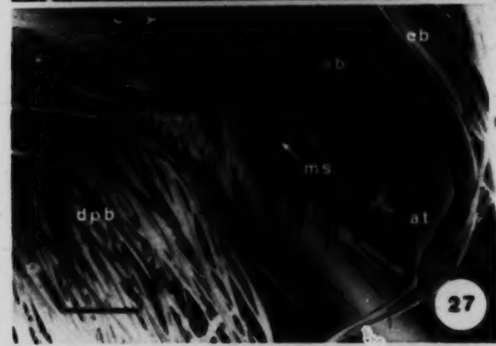
Figures 25 - 32. Structural features of the larva of *Parasimlium crosskeyi* Peterson (penultimate instar): (25) left antennal base (dorsal), scale = 40 µm; (26) labral fan rays (apicolateral), scale = 20 µm; (27) right mandible (aboral surface), scale = 20 µm; (28) hypostoma (ventral), scale = 50 µm; (29) prothoracic proleg (posterior), scale = 100 µm; (30) maxillary palpus (lateral), scale = 50 µm; (31) anal sclerite (terminal) scale = 100 µm; (32) posterior proleg (terminal), scale = 50 µm.

Abbreviations: ab = apical brush; at = apical tooth; bms = bacteria-covered multiporous sensillum; cb = covering brush; da = dorsal arm; d art = distal article; dms = dorsomedian sclerite; dpb = distal prosthecal brush; lfb = labral fan base; mab = membranous antennal base; mps = multiporous peg sensilla; ms = mandibular serrations; pp = posterior proleg; tp = terminal plate; va = ventral arm; vms = ventromedian sclerite.

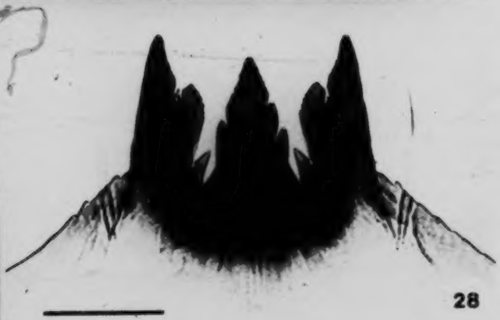

fb
mps
map
bms

25

26

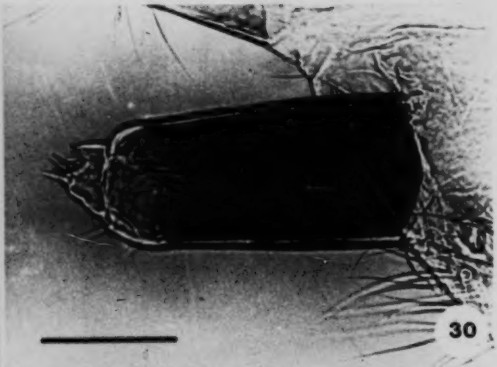

eb
sb
ms
dpb
at

27



28

29



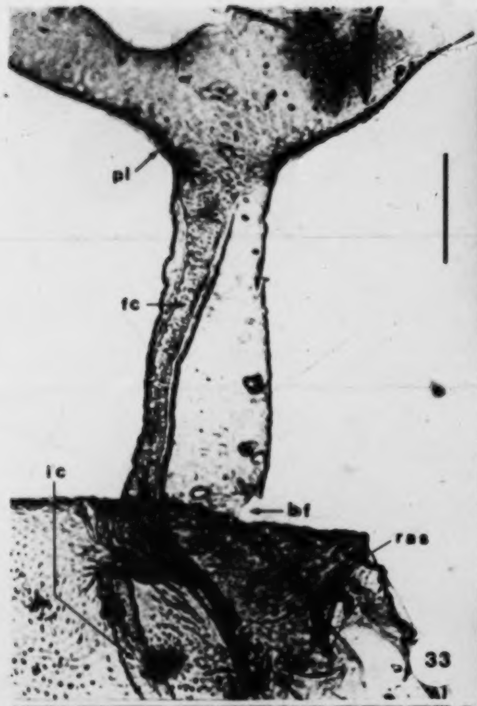
30

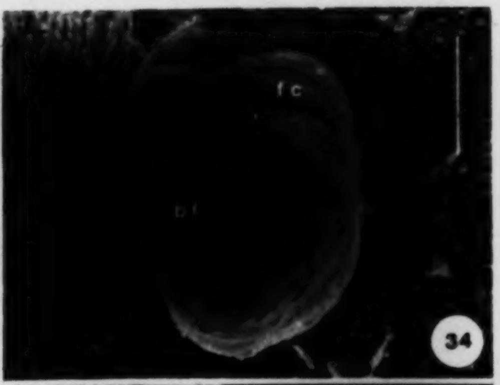
31

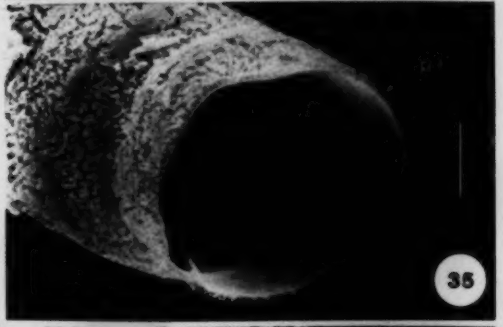
32

Figures 33 - 39. Structural features of the pupa of *Parasimulium crosskeyi* Peterson: (33) base of right respiratory organ (lateral), scale = 100 μm; (34) base of right respiratory organ (transverse), scale = 40 μm; (35) branch of respiratory organ (lateral-oblique), scale = 20 μm; (36) granules on portion of thorax (dorsolateral), scale = 10 μm; (37) abdominal segments 3 to 7 (dorsal), scale = 400 μm; (38) abdominal segments 6 - 9 (lateral), scale = 100 μm; (39) abdominal segments 4 to 7 (ventral), scale = 400 μm.

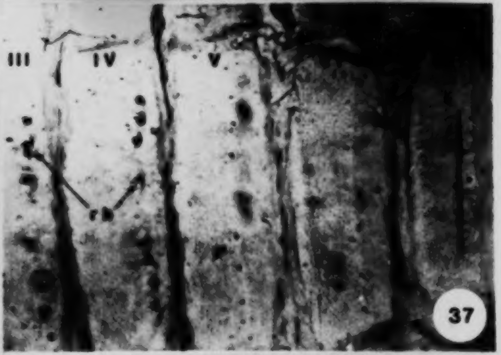
Abbreviations: bf = basal fenestra; ic = intercuticular tracheal connection; fc = felt chamber; pl = plastron; pl mem = pleural membrane; ras = regulatory apparatus of spiracle; rh = recurved hook; th = terminal hook.


pl
fc
lc
bf
ras
33

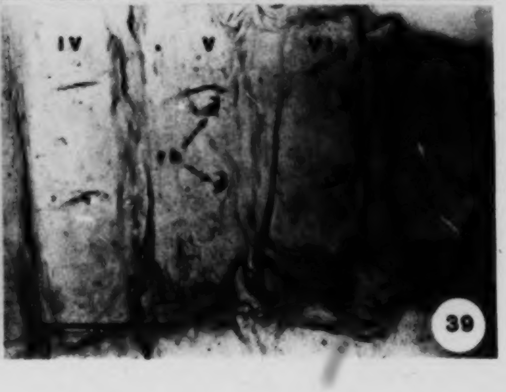

fc
bf
34


35

36

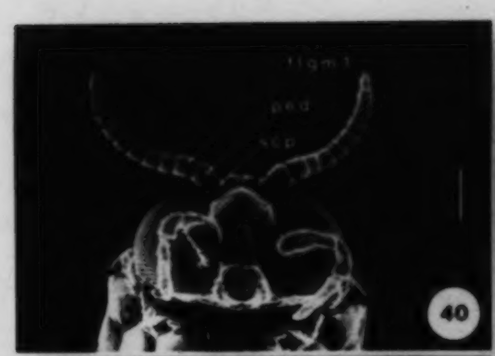

III
IV
V
rb
37

pl mem
38

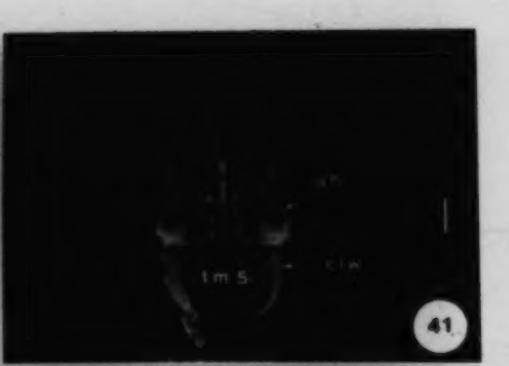

IV
V
VI
rb
39

Figures 40 - 47. (40) head of female of *Prosimulium sp*. (frontal), scale = 200 µm; (41) tarsomere 5 of male of *Parasimulium crosskeyi* Peterson (ventral), scale = 20 µm; (42) abdomen of male of *Prosimulium sp*. (dorsal), scale = 400 µm; (43) head of larva of *Simulium decorum* Walker (ventral), scale = 200 µm; (44) posterior margin of compound eye of male of *Parasimulium crosskeyi* Peterson (lateral), scale = 20 µm; (45) head of male of *Parasimulium crosskeyi* Peterson (frontal), scale = 200 µm; (46) ventral half of thorax of male of *Parasimulium crosskeyi* Peterson (lateral), scale = 200µm; (47) terminalia of male of *Parasimulium crosskeyi* Peterson (lateral), scale = 40 µm.

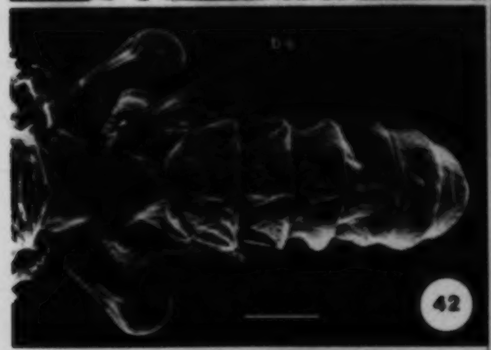
Abbreviations: anepst = anepisternum; bs = basal scale; clw = claw; cx = coxa; flgm = flagellomere; goncx = gonocoxite; gonst = gonostylus; gh = grappling hook; kapst = katepisternum; mf = median fan; ped = pedicle; pf = primary fan; sb = stemmatic bulla; scp = scape; sf = secondary fan; tm = tarsomere


flgm1
ped
scp

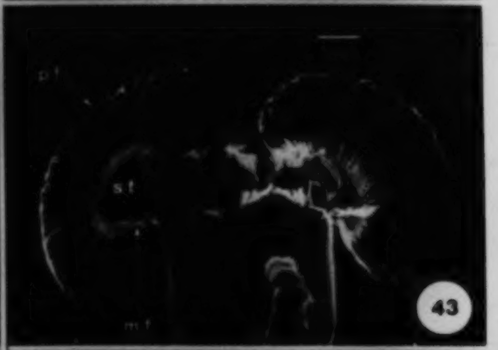
40



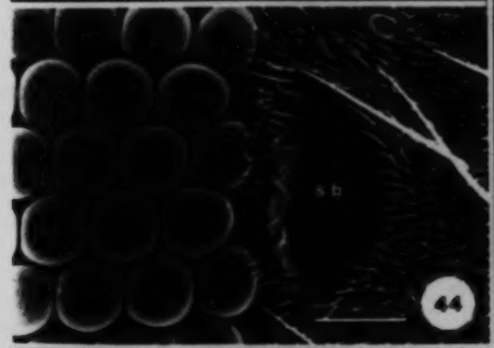
41



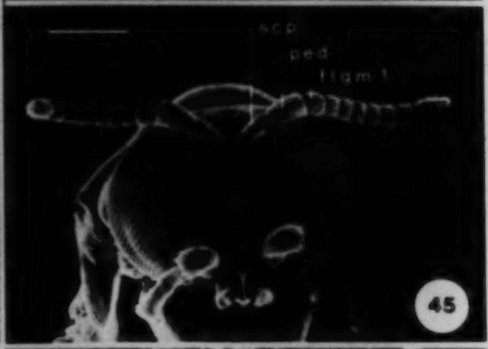
42



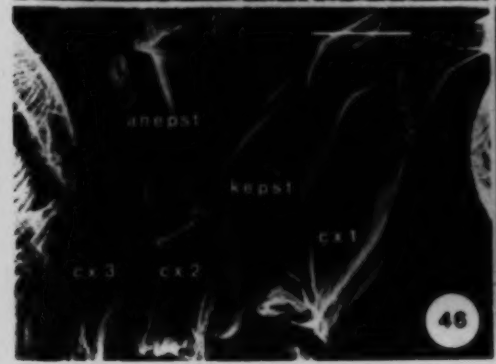
43



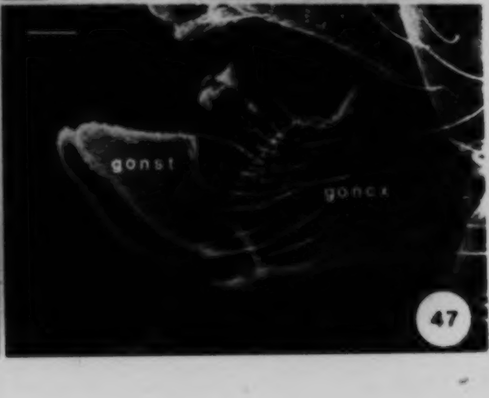
44


scp
ped
flgm1

45


anepst
kepst
cx1
cx3
cx2

46


gonst
goncx

47

Figures 48 - 55. (48) abdominal segments 8 and 9 of larva of *Parasimulium crosskeyi* Peterson (posteroventral), scale = 100 µm; (49) head of male of *Prosimulium* sp. (lateral), scale = 200 µm; (50) ventral half of thorax of female of *Prosimulium* sp. (lateral), scale = 100 µm; (51) abdominal segments 6 - 9 of pupa of *Prosimulium formosum* Shewell (ventral), scale = 200 µm; (52) abdominal segments 6 - 9 of pupa of *Prosimulium formosum* Shewell (lateral), scale = 400 µm; (53) anterior margins of abdominal segments 6 and 7 of pupa of *Prosimulium formosum* Shewell (dorsal), scale = 200 µm; (54) right antenna of larva of *Simulium decorum* Walker (dorsolateral), scale = 40 µm; (55) head capsule of larva of *Prosimulium alpestre* Dorogostaisky, Rubtsov & Vlasenko (ventral), scale = 20 µm.

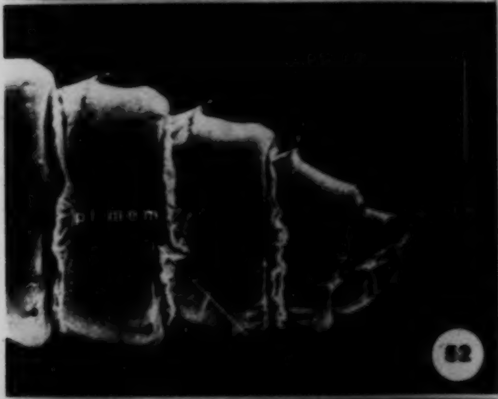
Abbreviations: anepst = anepisternum; ap = anal proleg (posterior proleg); cx = coxa; d art = distal article; hyp = hypostoma; kepst = katepisternum; k sulc = katepisternal suclus; lfb = labral fan base; m art = medial article; mps = multiporous peg sensilla; mvt = midventral tubercle; p art = proximal article; p clft = postgenal cleft; pl mem = pleural membrane; rh = recurved hook; sp cb = spine comb; st mem = sternal membrane; th = terminal hook; ucs = uniporous cone sensillum.

mv1
48

49

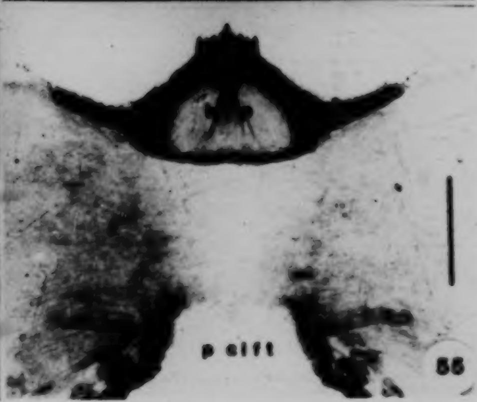
50

st mem
51


pl mem
52

sp cb
53

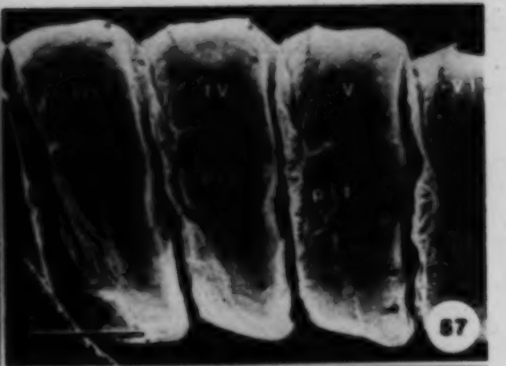
54


p clft
55

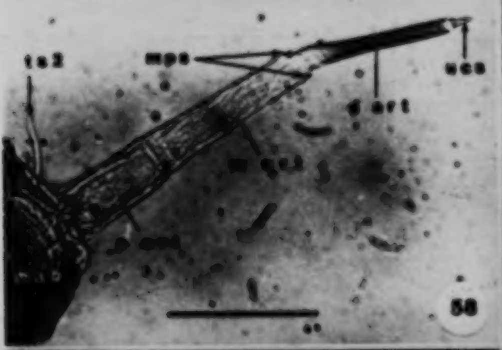
Figures 56 - 63. (56) prothoracic proleg of larva of *Simulium decorum* Walker (lateral), scale = 40 µm; (57) abdominal segments 3 to 6 of pupa of *Prosimulium formosum* Shewell (lateral), scale = 400 µm; (58) antenna of larva of *Prosimulium alpestre* Dorogostaisky, Rubtsov & Vlasenko (lateral), scale = 100 µm; (59) hypostomal teeth of larva of *Prosimulium mixtum/fuscum* complex (ventral), scale = 20 µm; (60) right maxillary palpus of first instar larva of *Prosimulium mixtum/fuscum* complex (lateral), scale = 5 µm; (61) mouthparts of first instar larva of *Prosimulium mixtum/fuscum* complex (frontal), scale = 50 µm; (62) tarsomeres 1 and 2 of hindleg of *Simulium* sp. (lateral), scale = 50 µm; (63) costa of female of *Simulium vittatum* Zetterstedt complex (dorsal), scale = 40 µm.

Abbreviations: aflp = apical fringe of lateral plate; apb = anteromedian palatal brush; clcp = calcipala; d art = distal article; hmt = hair-like macrotrichia; hyp = hypostoma; hyp teeth = hypostomal teeth; lp = lateral plate; m art = medial article; mnd = mandible; mps multiporous peg sensilla; mxl = maxilla; p art = proximal article; plt = pleurite; smt = spine-like macrotrichia; tm = tarsomere; ts = trichoid sensillum; ucs = uniporous cone sensillum

56



57


ts2
mps
ucs
d art
58

59

60

61

62

63

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2.13 Appendix 1

Taxa examined for characters used in analysis of primary evolutionary lineages of Simuliidae. Species names are provided for genus-group taxa with 5 or less species available for study. Only the total number of species examined is given for genus groups with 6 or more species available for study. Genera and subgenera listed here are essentially those recognized by Crosskey (1981, 1987) except that *Urosimulium* Contini is listed as a subgenus of Prosimuliini[13], and *Procnephia* Crosskey and *Paracnephia* Rubtsov are ranked as full genera of Simuliini[14].

Parasimuliinae

Parasimulium Malloch
    Parasimulium s. str.
        crosskeyi Peterson
        stonei Peterson

Simuliinae: Prosimuliini

Gymnopais Stone
        10 species
Levitnia Chubareva and Petrova
        freidbergi Beaucournu-Saguez & Braverman
Prosimulium Roubaud
    Distosimulium Peterson
        pleurale Malloch
    Helodon Enderlein
        7 species

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[13] Crosskey refers *Urosimulium* species to the "*Prosimulium s.str. aculeatum* group".

[14] Crosskey ranks *Procnephia* and *Paracnephia* as subgenera of *Prosimulium s.lat.*

- *Parahelodon* Peterson
  - *decemarticulatum* (Twinn)
  - *gibsoni* (Twinn)
  - *vernale* Shewell
- *Prosimulium s. str.*
  - 21 species
- *Urosimulium* Contini
  - *aculeatum* Rivosecchi

Twinnia Stone and Jamnback

- *hirticornis* Wood
- *hydroides* (Novák)
- *nova* (Dyar and Shannon)
- *tibblesi* (Dyar and Shannon)
- *sedecimfistulata* (Rubtsov)

Simuliinae: Simuliini

Araucnephia Wygodzinsky and Coscarón

- *montana* (Philippi)

Austrosimulium Tonnoir

- *Novaustrosimulium* Dumbleton
  - *bancrofti* (Taylor)

Cnephia Enderlein

- *dacotensis* (Dyar and Shannon)

Cnesia Enderlein

- *dissimile* (Edwards)

Crozetia Davies

- *crozetensis* (Womersley)

Ectemnia Enderlein

- *invenusta* (Walker)
- *taeniatifrons* (Enderlein)

Gigantodax Enderlein

- *kuscheli* (Wygodzinsky)

- *Greniera* Doby and David
  - *denaria* (Davies, Peteron, and Wood)
- *Mayacnephia* Wygodzinsky and Coscarón
  - *pachecolunai* (Leon)
  - *stewarti* (Coleman)
  - 'species X'; Currie, 1986
- *Metacnephia* Crosskey
  - *pallipes* (Fries) complex
  - *saskatchewana* (Shewell and Fredeen)
  - *villosa* (DeFoliart and Peterson)
- *Paracnephia* Rubtsov
  - *muspratti* (Freman and de Meillon)
- *Paraustrosimulium*
  - *anthracinum* (Bigot)
- *Procnephia* Crosskey
  - *morotoense* (McCrae and Prentice)
  - *rhodesianum* (Crosskey)
- *Stegopterna* Enderlein
  - *mutata* (Malloch) complex
  - 'cytospecies X'; Madahar, 1969
- *Tlalocomyia* Wygodzinsky and Díaz Nájera
  - *revelata* Wygodzinsky and Díaz Nájera
- *Simulium* Latreille
  - *Byssodon* Enderlein
    - *meridionale* Riley
  - *Eusimulium* Roubaud
    - *aureum* Fries
    - *baffinense* Twinn
    - *canonicolum* (Dyar and Shannon)
    - *duplex* Shewell and Fredeen
    - *euryadminiculum* Davies
  - *Hearlea* Vargas, Martinez Palacios and Díaz Nájera
    - *canadense* Hearle
  - *Hellichiella* Rivosecchi and Cardinali
    - *anatinum* Wood

excisum Davies, Peterson, and Wood
nebulosum Currie and Adler
Nevermannia Enderlein
6 species
Parabyssodon Rubtsov
transiens Rubtsov
Psilopelmia Enderlein
bivittatum Malloch
griseum Coquillett
Psilozia Enderlein
argus Williston
vittatum Zetterstedt
Shewellomyia Peterson
longistylatum Shewell
Simulium s. str.
13 species

3. MONOPHYLY AND RELATIONSHIPS OF GENUS-GROUP TAXA OF PROSIMULIINI (DIPTERA: SIMULIIDAE).

3.1 Synopsis

Eighty-one character states or character systems of larvae, pupae and adults are analyzed for evidence of monophyly and phyletic relationships of genus-group taxa of Prosimuliini. The following monophyletic genus groups are recognized, based on 2 or more hypothesized synapotypies each: *Prosimulium* Roubaud *s.str.* (66 species), *Helodon* Enderlein *s.str.* (13 species), *Parahelodon* Peterson (3 species), *Distosimulium* Peterson (2 species), *Urosimulium* Contini (3 species), *Levitinia* Chubareva & Petrova (2 species), *Twinnia* Stone & Jamnback (10 species), and *Gymnopais* Stone (12 species). Most previous concepts of *Prosimulium s.str.* and *Helodon s.str.* are shown to consist of non-monophyletic assemblages of species. *Prosimulium s.str.* is hypothesized to be the monophyletic sister taxon of all other Prosimuliini. Three major lineages are recognized within this latter assemblage as follows: (1) *Helodon s.str.*, (2) *Parahelodon* + *Distosimulium*, (3) *Urosimulium* + *Levitinia* + *Twinnia* + *Gymnopais*. Analysis of structural characters alone does not resolve relationships among these three clades. The partially resolved cladogram provides the information necessary to "root" published reconstructed cytological transformation series ("cytophylogenies"), which are derived from unrooted, hypothetical, "standard sequences" (*e.g.* Rothfels 1979). The resulting topology is used to test hypotheses about relationship, and to provide resolution where structural information alone has failed. This combination of morphological and cytological information yields a reconstructed phylogeny, providing the basis for a reclassification of Prosimuliini. The following system of genera and subgenera is adopted: *Prosimulium*, *Helodon s.lat.* (including the subgenera *Helodon s.str.*, *Parahelodon*, and *Distosimulium*), *Urosimulium*, *Levitinia*, *Twinnia*, and *Gymnopais*. The nominate subgenera *Parahelodon* and *Distosimulium* are relegated in new status from *Prosimulium s.lat.* to *Helodon s.lat.* A check list of world species of Prosimuliini is arranged according to the new classification, with 24 species relegated in new combination. Keys to larvae, pupae, and adults of genus-group taxa of Prosimuliini are provided.

3.2 Introduction

Resolution of the initial dichotomy of Simuliinae[1] has been one of the longest-standing problems facing black-fly systematists. The structural homogeneity of simuliids, and the difficulties in establishing apotypic and plesiotypic character states, have caused some authors to abandon completely the idea of a division based on phylogenetic relationships (*e.g.* Crosskey 1981, 1987). The resulting classifications divide Simuliinae into two more or less equally-sized tribes (*viz.* Prosimuliini and Simuliini), based on what is believed to be a sufficiently large phenetic gap between the two segregates. In essence, this division is between a well-defined monophyletic assemblage (the large, cosmopolitan genus *Simulium* Latreille *s.lat.*), and a polyphyletic assemblage comprising all other genera of Simuliinae. Although it is acknowledged that this type of arrangement is untenable in a phylogenetic system, Crosskey maintains that classifications are needed for every-day practical purposes, and that phylogeny should not destabilize a compromise classification which is based on "convenient", if unnatural, groupings. This is the system presently followed by most western European and North American black fly specialists.

Not all workers are satisfied with the current state of black-fly systematics. As indicated by Wygodzinsky and Coscarón (1973), establishment of a comprehensive cladistic system is fundamental to an understanding of the dispersal and evolutionary history of Simuliidae. With increasing application of phylogenetic techniques *sensu* Hennig, and with the advent of cytotaxonomic techniques as a convincing phylogenetic indicator (Rothfels 1979, 1981, 1987), relationships among genera of Simuliinae have become increasingly well understood. However, there have been very few attempts to resolve the initial dichotomies of Simuliinae using phylogenetic techniques, and fewer still to propose a suprageneric classification based on this hypothesized set of relationships. Rubtsov (1974), in his treatise on the evolution, phylogeny and classification of Simuliidae, identified three "monophyletic" lineages (as subfamilies) of Simuliinae, namely, the Gymnopaidinae (*Gymnopais*, *Twinnia*), the Prosimuliinae (*Prosimulium*, *Helodon*, *Urosimulium*, *Gigantodax*, *Procnephia*, and *Paracnephia*), and the Simuliinae (all remaining genera, exclusive of *Parasimulium*). He placed Gymnopaidinae as the sister taxon of the other two subfamilies combined, assuming that the fanless condition in larvae of *Gymnopais* and *Twinnia* is primitive. Unfortunately, most of Rubtsov's taxa are based on symplesiotypy, and cannot be upheld in a cladistic system (*cf.* chapter 2). Further, his notions about relationship is colored by the ill-founded conclusion that black flies are derived from a chironomid ancestor! No convincing evidence has been adduced to suggest such a relationship. Nevertheless, most Eastern European and Soviet specialists follow Rubtsov's suprageneric classification.

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[1] The subfamily Simuliinae is defined in the present work as all black-fly genera, exclusive of *Parasimulium s.lat.* Malloch (=Parasimuliinae).

In the previous chapter I analyzed ten characters that suggested the following initial dichotomy in Simuliinae: the tribe Prosimuliini (consisting of the genus groups *Prosimulium, Helodon, Parahelodon, Distosimulium, Urosimulium, Levitinia, Twinnia,* and *Gymnopais*), and the tribe Simuliini (consisting of all other genus groups of Simuliinae). Five synapotypies were provided as evidence of the monophyly of each of the two tribes. Prosimuliini includes 123 nominal species, distributed throughout the Holarctic region. The general focus of this chapter is to establish the monophyly of, and relationships among, the various genus-groups of Prosimuliini.

Phylogenetic studies have already been used to resolve sister-group relationships among some of the taxa included in Prosimuliini, as defined in chapter 2. For example, Wood (1978) provided convincing evidence that the so-called fanless black flies, belonging to the genera *Gymnopais* and *Twinnia*, are derived from a fully fanned *Prosimulium s.lat.* ancestor. Unfortunately, because of previous (and often divergent) interpretations about the limits of Prosimuliini, relationships among the majority of prosimuliine genus groups have yet to be satisfactorily resolved. This fundamental lack of understanding about phylogenetic relationships has resulted in greatly varied classificatory schemes, in which a particular assemblage may be ranked as a distinct genus in one system, but as a species-group in another. Such differences in opinion will exist as long as taxonomic limits are defined solely on the basis of phenetic differences and similarities. What might appear to be a substantial structural difference to one worker may seem trivial to another. A more universally accepted classification of Prosimuliini (and indeed of Simuliidae as a whole) can be achieved only through a better understanding of phylogenetic relationships.

Not only are relationships among the genus groups of Prosimuliini inadequately understood, but several of these aggregates (at least as currently defined by most workers) consist of largely non-monophyletic assemblages of species. Homoplasy is rampant among black flies, and so convenient structural "gaps" do not exist between all lineages. If all characters are considered simultaneously when assigning a species to one supraspecific taxon or another, and if all these character states are given equal taxonomic weight (*i.e.* without regard for whether they are primitive or derived), then the prospect of assigning a species to the correct monophyletic taxon is greatly impeded. Prosimuliine species can immediately be assigned to a correct genus group if only synapotypies are considered.

Recent advances in understanding of inter- and intra-familial relationships have rendered polarity decisions easier to make.

Cytological evidence has provided compelling evidence about relationships among several of the genus groups referred to Prosimuliini (Rothfels and Freeman 1966, Rothfels 1979). The technique essentially involves grouping species based on sequential rearrangements of chromosomes. Rearrangements such as inversions and interchanges are traced stepwise from a hypothetic "standard" or central sequence, providing evidence of the monophyly of groups of species derived from that standard. The rationale for such groupings is that complex rearrangements are the product of compounded, successive two-break steps of unique origin (Rothfels 1987). The resulting cytological transformation series ("cytophylogeny") is unrooted because the hypothetical standard sequence is established not from outgroup comparison, but rather from its centrality *i.e.* a composite of the central arrangement in each chromosome arm. Hence, the standard sequence should give rise to the largest possible number of independantly derived lineages. If one were able to root such a transformation series using morphological criteria, then the resulting set of relationships can be used as a test against the morphologically derived cladogram.

Despite the potential for integrating both cytological and cladistic techniques, there have been no attempts to incorporate such information into a comprehensive classificatory system. Resistance to this approach seems to stem from the fact that, although cytology may be a powerful indicator of relationship, there are too may discrepencies with conventional or phenetic morphotaxonomic wisdom (Crosskey 1987). However, as will be shown later, morphological and cytological transformation series may agree very closely in a cladistic framework.

The specific objectives of the present chapter are: (1) to establish the monophyly of each genus-group segregate of Prosimuliini using morphological (non-cytological) characters; (2) to forward an initial interpretation about phylogenetic relationships among these lineages; (3) to superimpose on the resulting cladogram the cytological transformation series of Rothfels (1979) to a) test relationships suggested by morphological characters alone, and b) help resolve relationships where morphological characters alone may have failed; (4) to use the resulting cladogram as the basis for a reclassification of the world species of Prosimuliini.

3.3 Materials and Methods

3.3.1 Materials

Taxa examined for structural features of Prosimuliini include representatives of all valid genus-group segregates of the tribe, as defined in the present work: *Prosimulium* Roubaud, *Helodon* Enderlein, *Parahelodon* Peterson, *Distosimulium* Peterson, *Urosimulium* Contini, *Levitinia* Chubareva & Petrova, *Twinnia* Stone & Jamnback, and *Gymnopais* Stone. A total of 44 of 123 species referred to Prosimuliini were examined; these are indicated by an asterisk in Appendix I. Character-state distributions in all other species were determined as far as possible from original descriptions and published illustrations. Material examined is mainly specimens in my own collection, and in the Canadian National Collection (CNC), Ottawa. Character-state distributions in *Urosimulium aculeatum* Rivosecchi are based, in part, on specimens from the British Museum (Natural History), London. Character-state distributions of *Levitinia freidbergi* Beaucournu-Saguez & Braverman are based on material from the Laboratory of Applied Parasitology and Zoology, Faculty of Medicine, Rennes, France. Specimens of the following species were made available for study by the Zoological Institute, Laboratory of Parasitology, Academy of Sciences, Leningrad, USSR: *Gymnopais bifistulatus* Rubtsov, *G. trifistulatus* Rubtsov, *G. lindneri* Rubtsov, *G. rubtzovi* Bobrova, *G. frontatus* Yankovsky, and *Twinnia sedecimfistulata* (Rubtsov).

3.3.2 Specimen preparation and illustration

Figures 28 - 34, and 37 - 41 are prepared from ethanol-preserved specimens. Methods used to handle and execute the illustrations have already been described in chapter 2. Figures 10 - 27 are reproduced, with permission, from the Manual of Nearctic Diptera, Volume 1 (cf. Peterson 1981). Cladograms and diagrammatic representations of character transformations are executed with the aid of a software program designed for a Macintosh™ microcomputer.

3.3.3 Classification

Six genera are included by me in the tribe Prosimuliini: *Prosimulium* Roubaud, *Helodon* Enderlein, *Urosimulium* Contini, *Levitinia* Chubareva & Petrova, *Twinnia* Stone & Jamnback, and *Gymnopais* Stone. Three subgenera are recognized in *Helodon* as follows: *Helodon s.str.*, *Parahelodon* Peterson, and *Distosimulium* Peterson. No classification of Prosimuliini so far proposed has this combination or arrangement of genus groups.

The genera *Levitinia*, *Twinnia*, and *Gymnopais*, as defined in the present work, reflect the concepts of most previous authors (*e.g.* Rubtsov 1964; Wood 1978; Peterson 1981; Crosskey 1981, 1987; Chubareva and Petrova 1981; Beaucournu-Saguez and Braverman 1987). My concept of the genus *Prosimulium* is more restricted than the sense used by most other authors (*e.g.* Rubtsov 1956, 1964; Crosskey 1987), corresponding more with the limits of Peterson's (1970) *Prosimulium s.str.* *Helodon s.lat.* is here defined in a comparatively broad sense, in accord with the opinion of Rothfels (1979) that the nominal taxa *Helodon s.str.*, *Parahelodon*, and *Distosimulium* are all derived cytologically from an immediate common ancestor. The subgenus *Helodon s.str.* is defined more broadly than in the sense of Rubtsov (1956, 1960, 1974), and more narrowly than in the sense of Crosskey (1987), corresponding more with the limits of *Helodon s.str. sensu* Peterson (1970). Limits of the subgenera *Parahelodon* and *Distosimulium*, as defined in the present work, are the same as those suggested by previous authors (Peterson 1970, 1981; Uemoto *et al.* 1976; Crosskey 1987); however, these two taxa are considered to be subgenera of *Helodon s.lat.*, rather than *Prosimulium s.lat.* Species belonging to the nominal taxon *Urosimulium* have variously been ranked at the level of genus by some workers (*e.g.* Contini 1963, Rivosecchi 1978, Rubtsov 1974), or as a mere species group of *Prosimulium s.str.* by others (*e.g.* Rothfels 1979; Crosskey 1969, 1987). Although the exact relationships of this lineage have yet to be firmly established, it is clear that *Urosimulium* belongs to a monophyletic assemblage of species whose sister group is *Prosimulium s.str.* Until the relationships of *Urosimulium* are more fully resolved, I prefer to rank this taxon as a genus. Justification for the system adopted in the present work will be given later.

It is convenient at various points throughout the text to refer to particular assemblages of genera. The term "fanless Prosimuliini" refers to the genera *Levitinia*, *Twinnia*, and *Gymnopais*, whose larvae are distinguished by the absence of labral fans in all instars. The term "fanned Prosimuliini" refers to genera whose larvae are characterized by well-developed labral fans in the second- through ultimate instars.

3.3.4 Terms

In this chapter I follow the general structural terms for Diptera as outlined by Teskey (1981). For structures that are unique (autapotypic) for Simuliidae, I have followed largely the terms of Peterson (1970,1981). Exceptions to this scheme, and additional terms used for specific stuctures of the larval head and abdomen, have been outlined in chapter 2, and will not be repeated here.

Both intra- and extra-cellular characters are used to resolve relationships among genus-group taxa of Prosimuliini. It is convenient to use the term "structural character" for non-chromosomal (non-cytological) features. Similarly, the term " structural synapotypy" refers to shared, derived, non-chromosomal characters.

3.3.5 Phylogenetic methods

The monophyly of genus groups of Prosimuliini, and phylogenetic relationships among these lineages, were determined using phylogenetic principles *sensu* Hennig (1966). My general approach to systematics is outlined in chapter 2.

Unlike the character analysis of the second chapter, which provided resolution of the initial two dichotomies of Simuliidae, I have not attempted to distinguish between different categories of synapotypy in this investigation of genus-group relationships among Prosimuliini. Primary- and secondary synapotypies are distinguished on the basis of their relative reliability as phylogenetic indicators, with the former being favored in phylogenetic reconstruction. Primary synapotypies must be both innovative and unique within Simuliidae, or be part of a functional complex. Further, a primary synapotypy cannot be homoplastic within Culicomorpha. The criteria for secondary synapotypies are not as strict, and such features can either be provided only as support for hypotheses based on primary characters, or be interpreted in view of relationships suggested by primary characters. Such strict criteria for asserting synapotypy can be applied only to higher taxa of subfamily level and up (Sæther 1986). All possible synapotypies, including those that are homoplastic in Simuliidae, are considered in the present investigation. Careful reference is made to the immediate out-groups when homoplastic characters are analyzed, to ensure that the correct polarity decision is made.

Structural synapotypies are used to form an initial hypothesis about the monophyly and relationships of Prosimuliini genus groups. The resulting topology provides the basis by which the cytological transformation series of Rothfels (1979; figs. 2,3, and 4) can be rooted. The rooted transformation series is then used to falsify or support hypotheses of relationship based on structural characters alone, and may also provide resolution where structural characters alone have failed.

3.4 Monophyly, sister-group relationship, and groundplan of Prosimuliini

Tribe **Prosimuliini** Enderlein

PROSIMULIINAE Enderlein, 1921: 199. Type genus: *Prosimulium* Roubaud, 1906.
HELLICHIINI Enderlein, 1925: 203. Type genus: *Hellichia* Enderlein, 1925.
GYMNOPAIDINAE Rubtzov, 1955: 329, 330. Type genus: *Gymnopais* Stone, 1949.
HELODONTINI Ono, 1982: 280, 282. Type genus: *Helodon* Enderlein, 1921.

Diagnosis: *Male and Female*: Rs distinctly forked, forked portion conspicuously longer than its petiole; C with uniformly-sized hair-like macrotrichia only, without thickened or spiniform macrotrichia interspersed among them. Calcipala and pedisulcus absent. *Male*: ventral plate of aedeagus typically with strap-like connection between apex of anterolateral apodeme and paramere (paramere not connected to ventral plate in *Distosimulium, Parahelodon,* and *Levitinia*); paramere simple apically, without accessory spines. *Pupa*: Abdominal segments 4 and 5 with large pleural plates (pleurites) laterally, these separated from terga and sterna of same segments by paired longitudinal bands of striate membrane (pleurite present only on segment 5 of *Levitinia*); segment 3 either without pleural membrane (segment ring-like), or membrane in form of single narrow longitudinal band. *Larva*: Antenna with proximal and medial articles unpigmented, contrasted with black distal article. Hypostoma lacking paralateral teeth. Anteromedian palatal brush of first-instar of scoop-shaped, fringed plates. Maxillary palpal sensilla of first-instar subapically situated and in a linear configuration.

In chapter 2, I provided 5 characters in support of the monophyly of Prosimuliini. The tribe includes the following genus-group taxa of Simuliidae: *Prosimulium* Roubaud *s.str.*, ***Helodon*** Enderlein *s.str.*, ***Parahelodon*** Peterson, ***Distosimulium*** Peterson ***Urosimulium*** Contini ***Levitinia*** Chubareva & Petrova, ***Twinnia*** Stone & Jamnback and ***Gymnopais*** Stone. Excluded from Prosimuliini are the nominal taxa ***Procnephia*** Crosskey and ***Paracnephia*** Rubtsov, which have formerly been considered to be closely related to ***Prosimulium*** (*e.g.* Rubtsov 1974, Crosskey 1969, 1981, 1987). I have relegated these two segregates, along with all remaining genus-groups of Simuliinae, to Simuliini.

Prosimuliini is placed as the sister taxon of Simuliini, and this entire assemblage is placed as the sister taxon (Simuliinae) of *Parasimulium s.lat.* (Parasimuliinae). Parasimuliinae is the plesiotypic out-group, and Simuliini is the apotypic out-group. Polarity decisions are made primarily with respect to the sister-group relationships outlined above. Reference to other Culicomorpha is made when the direction of character polarity remains uncertain.

Groundplan apotypies of Prosimuliini have been discussed in detail in chapter 2. Therefore, constitutive features are enumerated below with little further comment, other than a statement about the hypothesized primitive state. These same numbers appear on the concluding cladogram (fig. 3).

Character 1.

Pupal abdomen with large pleural plates (pleurites) on segments 4 and 5. — The primitive state is pleurites inconspicuous, or absent.

Character 2.

Larval antenna with proximal and medial articles unpigmented, contrasted with black distal article. — The primitive state is basal 2 articles with at least some pigmentation, not contrasted sharply with color of distal article.

Character 3.

Larval hypostoma lacking paralateral teeth. — The hypostomae of all other Simuliidae larvae possess one or more paralateral teeth, which is considered primitive.

Character 4.

Anteromedian palatal brush of first-instar larva consisting of scoop-shaped, fringed plates. — The primitive state is anteromedian palatal brush of first-instar larvae of simple hairs.

Character 5.

Maxillary palpal sensilla of first-instar larva subapically situated and in a linear configuration. — The maxillary palpal sensilla are primitively arranged in a circular fashion on the apex of the palp.

3.5 Keys to genus groups of Prosimuliini of the world

3.5.1 Key to females of Prosimuliini

1. Hypogynial valve relatively long and narrowly rounded or pointed apically, extended posteriorly to level of anal lobe, or beyond (giving abdomen a pointed appearance posteriorly); anteromedial corner of each valve produced nipple-like. Spermatheca with large differentiated area at junction with spermatheca duct (fig. 10). ....*Prosimulium* Roubaud

— Hypogynial valve relatively short and truncated apically, not extended posteriorly to level of anal lobe (giving abdomen a truncated appearance posteriorly); anteromedial corner of each valve not produced nipple-like. Spermatheca variable (figs. 11-15). ... 2

2. Tarsal claw simple, or at most with small, inconspicuous, basal or subbasal tooth (fig. 26). Posteromedial margin of compound eye with a distinct, shiny, raised, stemmatic bulla (fig. 23). Antenna with 7 (rarely 8) flagellomeres. 3

— Tarsal claw with variously sized, but conspicuous, basal or subbasal tooth (fig. 27). Posteromedial margin of compound eye without a distinct stemmatic bulla (a suggestion of a bulla may be present in certain species of *Helodon s.str.*). Antenna typically with 9 (rarely 7 or 8) flagellomeres[1]. 4

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[1] Adults of *Helodon* (*Parahelodon*) *decemarticulatus* have an 8-articled flagellum, and adults *Helodon* (*Parahelodon*) *gibsoni* have a 7-articled flagellum.

3. General vestiture of sparse, short, erect setae. Clypeus bare except few erect setae laterally (fig. 23). Postnotum small and markedly arched, typically with distinct median longitudinal ridge (fig. 25). Mesepimeron with vestiture (= mesepimeral tuft) confined to dorsal part of sclerite above level of metathoracic spiracle (fig 24). Wing membrane smoky brown or grey (nearly opaque in some specimens), and slightly wrinkled; petiole of M_{1+2} elongate, about half as long as petiole of Rs (cf. fig. 20, Chapter 2). Terminal plate of genital fork not connected directly to tergum 9. Spermatheca strongly sclerotized, joined to spermathecal duct by short or long neck. Anal lobe and cercus fused into a single, solid sclerite (fig. 15). ….. *Gymnopais* Stone

— General vestiture of dense covering of recumbent setae (pile). Clypeus covered with setae. Postnotum larger, evenly arched, without median longitudinal ridge. Mesepimeron with vestiture more extensive, extended ventrally to area below level of metathoracic spiracle. Wing membrane hyaline and comparatively smooth; petiole of M_{1+2} short, much less that half as long as petiole of Rs. Terminal plate of genital fork connected directly to tergum 9. Spermatheca relatively slightly sclerotized and mushroom shaped, with a large area of differentiated membrane at junction with spermathecal duct. Anal lobe and cercus distinctly separated by membrane (fig. 14). ……………………………………………………………*Twinnia* Stone & Jamnback

4. Tergite 9 elongated and shield-like apically, projecting posteriorly well beyond apex of cercus. Spermatheca wider than long and mushroom shaped, with large area of differentiated membrane at junction with spermathecal duct (*e.g.* fig. 14). …………………………………………………………… *Levitinia* Chubareva & Petrova

— Tergite 9 short and blunt apically, not projected posteriorly as far as cercus. Spermatheca as long or longer than wide and not mushroom shaped; either in form of a markedly enlarged, delicate, unpigmented bag (fig. 13), or with (at most) a small circular area of differentiated membrane at junction with spermathecal duct (fig. 11)... 5

5. Cercus elongate (much longer than wide), tapered apically to fine point.
.... *Urosimulium* Contini

— Cercus short (much wider than long), broadly rounded or truncated apically (figs. 11-13). ....*Helodon s.lat.* Enderlein. ... 6

6. Arm of genital fork terminating in a greatly pronounced terminal plate that bears a patch of setae. Spermatheca a greatly enlarged, thin, delicate, unpigmented bag (fig. 13).
.... *Helodon* (*Distosimulium* Peterson)

— Arm of genital fork terminated in a variously sized terminal plate, without patch of setae. Spermatheca relatively small and variously pigmented; if spermatheca lightly pigmented, then with a distinct reticulate pattern (figs. 11-12). 7

7. Arm of genital fork relatively slender, terminated in pronouced wrinkled or denticulate terminal plate. Spermatheca semicircular to pear-shaped, heavily sclerotized, smooth (fig. 12). .... *Helodon* (*Parahelodon* Peterson)

— Arm of genital fork relatively wide, gradually expanded distally into plate not wrinkled or denticulate, but instead densely sclerotized and with acutely pointed, posteromedially directed, process. Spermatheca typically elongate, lightly sclerotized; if somewhat rounded, then spermatheca with a distinct reticulate pattern (fig. 11).
.... *Helodon* (*Helodon* Enderlein)

3.5.2 Key to males of Prosimuliini

1. Posteromedial margin of compound eye with a distinct, shiny, raised, stemmatic bulla (fig. 23). Antenna consisting of 7 (rarely 8) flagellomeres. 2

— Posteromedial margin of compound eye without a distinct stemmatic bulla (a suggestion of a bulla may be present in certain species of *Helodon s.str.*). Antenna typically consisting of 9 (rarely 7 or 8) flagellomeres[2]. 3

2. General vestiture of sparse, short, erect setae. Clypeus bare except few erect setae laterally (fig. 23). Postnotum small and markedly arched, typically with distinct median longitudinal ridge (fig. 25). Mesepimeron with vestiture confined to dorsal part of sclerite above level of metathoracic spiracle (fig. 24). Wing membrane smoky brown or grey (nearly opaque in some specimens), and slightly wrinkled; petiole of M_{1+2} elongate, about half as long as petiole of Rs (cf. fig. 20, chapter 2). Body of ventral plate of aedeagus not markedly emarginated laterally near base of anterolateral apodeme. Gonostylus slender, tapered posteriorly to fine point, with two or more minute apical setae easily resolved under magnification with dissecting microscope (fig. 22). .... *Gymnopais* Stone

— General vestiture of dense covering of recumbent setae (pile). Clypeus covered with setae. Postnotum larger, evenly arched, without median longitudinal ridge. Mesepimeron with vestiture more extensive, extended ventrally to area below level of metathoracic spiracle. Wing membrane hyaline and comparatively smooth; petiole of

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[2] Adults of *Helodon* (*Parahelodon*) *decemarticulatus* have an 8-articled flagellum, and adults *Helodon* (*Parahelodon*) *gibsoni* have a 7-articled flagellum.

M_{1+2} short, much less that half as long as petiole of Rs. Body of ventral plate of aedeagus markedly emarginate laterally near base of anterolateral apodeme. Gonostylus more robust, tapered posteriorly to broadly rounded point, with a single (rarely two) apical seta easily resolved under magnification with a dissecting microscope (fig. 21). ....*Twinnia* Stone & Jamnback

3. Ventral plate of aedeagus with anteromedial margin produced dome-like, projecting anteriorly nearly as far as apex of anterolateral apodeme. Paramere in the form of a narrow sclerotized bar that is intimately fused to gonocoxal apodeme. .... *Levitinia* Chubareva & Petrova

— Ventral plate of aedeagus with anteromedial margin either not markedly produced anteriorly (*i.e.* not produced anteriorly nearly as far as apex of anterolateral apodeme) (figs. 16-17), or produced as elongate, digiform, process projected anteriorly far beyond apex of anterolateral apodeme (fig. 18). Paramere better developed than above (either plate- or spine-like), typically connected to gonocoxal apodeme by slender arm[3]. 4

4. Gonostylus with accessory lobe laterally at base. .... *Urosimulium* Contini

— Gonostylus simple, without accessory lobe laterally at base (figs. 16-22). 5

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[3] Males of *Parahelodon* have the paramere fused along its entire base with the gonocoxal apodeme; however, the connection between these two structures is not as strong as it is in males of *Levitinia*.

5. Ventral plate of aedeagus not noticeably compressed or flattened dorsoventrally; apical margin with prominent ventrally directed lip or emargination (fig. 16). .... *Prosimulium* Roubaud

— Ventral plate of aedeagus compressed or flattened dorsoventrally; apical margin with, at most, short, ventrally directed lip, or none (figs. 17-18, 20-22). .... *Helodon s.lat.* Enderlein. 6

6. Ventral plate of aedeagus H-shaped, deeply cleft apically and with anterolateral apodemes relatively long. Median sclerite prolonged apically, projected posteriorly and ventrally well beyond posterior margin of ventral plate. Gonostylus with apical half markedly narrower than proximal half, tapered apically to fine point (fig. 20). Flexing action of gonostylus in dorsoventral plane. Paramere in form of dorsoventrally curved spine-like structure apposed apically with the tip of the gonostylus (fig. 19). .... *Helodon* (*Distosimulium* Peterson)

— Ventral plate of aedeagus neither deeply cleft apically, nor H-shaped. Median sclerite not produced apically beyond posterior margin of ventral plate. Gonostylus evenly tapered from base to apex, terminated in narrowly- to broadly-rounded point. Flexing action of gonostylus more in lateromedial plane. Paramere not in form of dorsoventrally curved spine-like structure that is apposed apically with tip of gonostylus (figs. 17-18). 7

7. Ventral plate of aedeagus with digiform dorsomedial projection basally, to which base of median sclerite is fused. Anterolateral apodeme short, pointed, slender. Median sclerite not Y-shaped apically, arms closely approximated to each other as a single,

solid structure. Paramere not connected to anterolateral apodeme by strap-like connection. Gonostylus with a single apical seta (fig. 18). .... *Helodon* (*Parahelodon* Peterson)

— Ventral plate of aedeagus without digiform dorsomedial projection basally; base of ventral plate either simple dorsomedially, or with, at most, a short rounded projection to which base of median sclerite is fused. Anterolateral apodeme longer and broader. Median sclerite distinctly Y-shaped apically, the arms well separated from each other. Paramere connected to anterolateral apodeme by strap-like connection. Gonostylus with 2 or more apical setae (fig. 17). .... *Helodon* (*Helodon* Enderlein)

3.5.3 Key to pupae of Prosimuliini

1. Abdominal terga 4 to 8 each without anterior row of closely set, posteriorly directed, spines (= spine combs); terga 3 and 4 each with three or fewer pairs of recurved hooks (figs. 7c, 7d). Abdominal segment 3 ring-like, pleurite fused to adjacent tergum and sternum (figs. 6c, 6d). 2

— Abdominal terga 6 to 9 at least, each with anterior row of closely set, posteriorly directed, spines (= spine combs); terga 3 and 4 each with 4 pairs of recurved hooks (fig. 7a, 7b). Abdominal segment 3 either with pleurite distinctly separated from adjacent tergum (membranous band narrow, longitudinally striated) (fig. 6a), or with pleurite absent (tract of striate membrane between tergum and sternum wide) (fig. 6b). 3

2. Abdominal sterna 3 and 4 each without recurved hooks; sterna 5 to 7 each with only 1 or 2 pairs of recurved hooks (fig. 8b). Abdominal terga 3 and 4 each with 3 pairs of markedly developed recurved hooks (fig. 7b). Abdominal segment 4 with pleurite separated from adjacent tergum and sternum by narrow, longitudinally striated, membranous band (fig. 6c). Gill of 16 filaments from 2 or 3 main trunks (fig. 29). Cocoon in the form of slimy envelope, all of pupa and larval exuviae enclosed. .... *Twinnia* Stone & Jamnback

— Abdominal sternum 3 with or without recurved hooks; sterna 4 to 7 each with 2 to 5 pairs of recurved hooks (fig. 8c). Abdominal terga 3 and 4 (and on segment 5 of some specimens) each with only 1-3 pairs of fine recurved hooks (fig. 7c). Abdominal segment 4 with pleurite not clearly differentiated from adjacent tergum, and only slightly differentiated from adjacent sternum (fig. 6d). Gill of maximum of 6 filaments (fig. 28). Cocoon in form of a small ventral pad, naked pupa attached by ventral abdominal hooks. .... *Gymnopais* Stone

3. Abdominal terga 4 and 5 each without anterior row of posteriorly directed spines (= spine combs) (fig. 7b). Abdominal segments 3 and 4 each without pleurite, the tergum and sternum of those segments separated by wide tract of longitudinally striated membrane (fig. 6b). .... *Levitinia* Chubareva & Petrova

— Abdominal terga 4 and 5 each with anterior row of posteriorly directed spines (= spine combs) (fig. 7a). Abdominal segments 3 and 4 each with large pleurite; pleurite of segment 3 fused with adjacent sternum, but distinctly separated from adjacent tergum by narrow, longitudinally striated, membranous band; pleurite of segment 4 clearly isolated, separated from adjacent tergum and sternum by narrow, longitudinally striated, membranous band (fig. 6a). .... *Prosimulium* Roubaud

Urosimulium Contini
Helodon (*Helodon* Enderlein)
Helodon (*Parahelodon* Peterson)
Helodon (*Distosimulium* Peterson)

3.5.4 Key to larvae of Prosimuliini (final instar)

1. Labral fans absent. Head capsule with lateral margins markedly convex in dorsal view, tapered anteriorly to conical labrum, latter terminated in a markedly pronouced palatal brush. Postgenal cleft rudimentary (figs. 30-31). Anal sclerite Y-shaped (fig. 9d) or inverted star-shaped, of 5 radiating arms of approximately equal length (fig. 9c). 2

— Labral fans present (may be adducted, but with bases obvious). Head capsule with lateral margins less convex in dorsal view. Postgenal cleft clearly developed (figs. 32-34). Anal sclerite X-shaped (fig. 9a) or subrectangular-shaped (the anterodorsal and posteroventral arms being reduced in length); if anal sclerite of 5 radiating arms, then posteromedial arm appearing conspicuously shorter than others (fig. 9b). 4

2. Antenna with basal two articles pigmented. Hypostoma with lateral serrations in form of spiniform setae. Anal sclerite inverted star-shaped, of 5 radiating arms (fig. 9c). .... *Levitinia* Chubareva & Petrova

— Antenna with basal two articles colorless (figs. 30-31). Hypostoma with lateral serrations in form of narrowly rounded denticulations. Anal sclerite Y-shaped (fig. 9d). 3

3. Cephalic apotome with median spots extended anteriorly to point below posterior-most eyespot. Labrum with lateral margins each with prominent bulge (fig. 31). Mandible with 10 or more rows of spine-like scales on anteroventral surface (fig. 36).
.... *Gymnopais* Stone

— Cephalic apotome with median spots extended anteriorly to level of anterior-most eyespot. Labrum with lateral margins without a prominent bulge (fig. 30). Mandible without numerous rows of spine-like scales on anteroventral surface; with, at most, a few spine-like setae immediately basad of apical mandibular (fig. 35).
....*Twinnia* Stone & Jamnback

4. Prothoracic proleg with lateral plate in form of narrow bar parallel to base of hooks, extended at most one-third the distance to base of apical article (fig. 40). 5

— Prothoracic proleg with lateral plate better developed than above, extended one-half or more distance to base of apical article (fig. 41). ....*Prosimulium* Roubaud

5. Antenna with basal two articles colorless (figs. 32-34). Anal sclerite without short, posteriorly-directed process from area between the posteroventral arms (fig. 9a).
.... *Helodon s.lat.* Enderlein ..6

— Antenna with basal two articles pigmented. Anal sclerite with short, posteriorly-directed process or arm from area between the posteroventral arms (fig. 9b).
.... *Urosimulium* Contini

6. Hypostoma with apex of median tooth at about same level as, or posterior to, those of posterior-most sublateral and lateral teeth (figs. 38-39). Postgenal cleft inverted U- or inverted V-shaped (figs. 32, 34). 7

— Hypostoma with apex of median tooth distinctly anterior to that of posterior-most sublateral tooth, and at about the same level of, or extended anteriorly beyond, apex of lateral tooth (fig. 37). Postgenal cleft biarctate, or subrectangular with faint anterior margin (fig. 33). .... *Helodon* (*Helodon* Enderlein)

7. Hypostoma with apices of teeth extended progressively more anteriorly from lateral tooth to inner-most sublateral tooth, anterior margin of hypostoma convex in form (fig. 39). Cephalic apotome with spots surrounded by dark-brown pigmented area, contrasting sharply with lighter yellowish color anteriorly. Postgenal cleft relatively broad and deep, extended anteriorly nearly one-half distance from posterior tentorial pits to hypostomal groove (fig. 32). .... *Helodon* (*Distosimulium* Peterson)

— Hypostoma with apices of teeth either extended progressively more posteriorly from lateral tooth to inner-most sublateral tooth, or apices of lateral and sublateral teeth extended anteriorly to about same level, anterior margin of hypostoma concave or flat (fig. 38). Cephalic apotome with spots surrounded by a lightly pigmented area, not contrasted sharply with brownish color anteriorly. Postgenal cleft relatively narrow and shallow, extended anteriorly no farther than about one-third distance from posterior tentorial pits to hypostomal groove (fig. 34). ....*Helodon* (*Parahelodon* Peterson)

3.6 Monophyly of genus-group taxa of Prosimuliini

3.6.1 Genus ***Prosimulium*** Roubaud

PROSIMULIUM ROUBAUD, 1906: 521. Type species *Simulia hirtipes* Fries, by subsequent designation of Malloch, 1914, *Technical Series. United States Department of Agriculture. Bureau of Entomology* **26**:16.

HELLICHIA ENDERLEIN, 1925: 203. Type species: *Hellichia latifrons* Enderlein,1925, by original designation.

TAENIOPTERNA Enderlein, 1925: 203. Type species *Melusina macropyga* Lundström, 1911, by original designation.

MALLOCHELLA Enderlein, 1930: 91. Type species: *Mallochella sibirica* Enderlein, 1930 [=*Simulia hirtipes* Fries, 1824], by original designation. Junior homonym, preoccupied by *Mallochella* Duda, 1925.

MALLOCHIANELLA Vargas & Díaz Nájera, 1948: 67. Replacement name for *Mallochella* Enderlein, 1930, preoccupied.

The genus *Prosimulium* Roubaud is the largest segregate of the tribe Prosimuliini, comprising no fewer than 66 valid species (Appendix 1). Its members are distributed throughout the Holarctic region, including the most northerly (Bjørnøya) and southerly (Morocco) records of the tribe.

The generic concept used here is rather more narrow than those favored by Rubtsov (1956, 1974) and Crosskey (1987) (as subgenus), and corresponds more closely with the one used by Peterson (1970) for the North American species of *Prosimulium s.str*. The first two mentioned authors refer to *Prosimulium* a number of species that have a well-developed basal or subbasal tooth on the female tarsal claw, which, as will be discussed later, is considered to be a groundplan apotypy of Prosimuliini, exclusive of *Prosimulium*. Further, prosimuliines with a toothed female claw lack any of the 4 synapotypies used to define *Prosimulium* (see below). Hence, it is clear that most previous concepts of *Prosimulium* are non-monophyletic, and cannot be accepted in a cladistic system.

Cytologically there are five major groups of *Prosimulium* species (Rothfels 1979): (1) the Palaearctic *P. hirtipes* group ("C_t"), (2) the Nearctic *P. mixtum* group ("IIIL-1"), (3) the western Nearctic *P. esselbaughi* group ("IIIL-2"), (4) the Nearctic *P. magnum* group ("IIIS-3"), and (5) the northern Holarctic *P. macropyga/ursinum* group. This last-mentioned group is the only one that does not have a distinctive cytological marker. The phylogenetic relationships among these five groups has not as yet been satifactorily resolved, either cytologically or cladistically. A satisfactory arrangement of named species groups within *Prosimulium* must therefore await further study.

Species assigned to *Prosimulium* based on purely cytological grounds (Rothfels 1979) closely reflects the arrangement proposed here, based on external structural characters. The only exception is the placement of *Urosimulium stefanii* Contini (= *U. aculeatum* Rivosecchi), which Rothfels suggests might belong to the Palaearctic *P. hirtipes* group. *Urosimulium* species share none of the synapotypies listed below for *Prosimulium*, and instead have the single constitutive feature listed for Prosimuliini, exclusive of *Prosimulium* (*viz.* presence of a distinct basal or subbasal tooth on the female tarsal claw). Rothfels did not provide any justification for his placement of *U. stefanii* in *Prosimulium*, although it would seem that his decision was based on the chromosome map published by Frizzi *et al.* (1970). P. H. Adler (personal communication) was unable to find convincing evidence about the relationships of *U. stefanii* based on his examination of this same map. Evidence presented later will show that *Urosimulium* is more likely the sister taxon of the fanless prosimuliines (*Levitinia, Twinnia,* and *Gymnopais*).

Ecologically, members of *Prosimulium* are the most diverse prosimuliine genus group. The immature stages live in a wide variety of running-water habitats: from tiny headwater springs, to large rivers; and from food-rich lake outflows, to oligotrophic alpine streams. Adult females primarily blood-feed upon mammals, although several northern species possess weakly developed mouthparts, and are therefore presumed to be autogenous (*e.g. Prosimulium neomacropyga* Peterson).

Monophyly of the genus *Prosimulium* Roubaud.

Character 6.

Hypogynial valves long, with anteromedial corner produced nipple-like. — Females of *Prosimulium s.str.* are distinguished from all other Prosimuliini females by the form of the hypogynial valves. These paired processes, which arise from near the posterior margin of the hypogynium (= sternum 8), may be homologous with the anterior gonapophysis of the orthopteroid ovipositor (McAlpine 1981). In *Prosimulium* these valves are relatively long and narrowly rounded or pointed apically, and project posteriorly to the level of the anal lobe (= sternum 10), or beyond (fig. 10). This arrangement gives the female abdomen a rather pointed appearance terminally. Another distinctive feature is that the anteromedial corner of each valve is produced nipple-like. In other Prosimuliini the valves are markedly shorter and more truncated posteriorly, and they do not project posteriorly as far as the anal lobes (figs. 11-15). The consequence of this arrangement is an abdomen that is rather more blunt apically. Further, the anteromedial corner of each valve is not produced nipple-like, and instead appears rather truncated. The condition in Prosimuliini exclusive of *Prosimulium* is also characteristic of *Parasimulium* and most Simuliini, and must therefore be considered primitive (**0**). Examination of out-group families (Thaumaleidae, Ceratopogonidae, Chironomidae) corroborates this conclusion.

The derived condtion, as found in *Prosimulium* (**1**), is also evident in some distantly related Simuliini (*e.g. Simulium* subgenus *Hemicnetha*), but this is undoubtedly an independently derived condition, as judged from other characters.

Character 7.

Spermatheca with large differentiated area at junction with spermathecal duct. — The spermatheca is a highly varied structure in Simuliidae, and has been used as a definitive character at various taxonomic levels (*e.g.* Peterson 1970, Wygodzinsky and Coscarón 1973). However, the pattern of variation is extremely complex, and much of this complexity is undoubtedly owing to parallelisms or reversals. This is true even within Prosimuliini, where no arrangement can be constructed that completely eliminates homoplasy. Conclusions about the direction of character evolution must therefore be made with caution. Based on out-group comparison with other Culicomorpha, it is clear that the groundplan for Simuliidae is for the spermatheca to be either complete basally (*i.e.* with no differentiated membranous area at junction with spermathecal duct), or to have only a small rounded area of differentiated membrane at the junction of the spermathecal duct (**0**). Such a condition is found in *Parasimulium* and many Simuliini. In Prosimuliini, the primitive condition is characteristic of *Helodon s.str.*, *Urosimulium*, *Parahelodon*, and *Gymnopais* (figs. 11, 12, 15). A spermatheca with a large differentiated circular area at the junction with the spermathecal duct must therefore be derived, and can be taken as evidence of the monophyly of *Prosimulium* (**1**). The only other Prosimuliini with a similar condition are *Levitinia* and *Twinnia* (fig. 14); however, this is probably an independently derived feature, as judged from other characters.

Character 8.

Ventral plate of aedeagus not flattened dorsoventrally, with a prominent lip or emargination apicoventrally. — Wood and Borkent (1982) suggested homologies between the ventral plate of male Simuliidae and variously named structures of other male Culicomorpha. Ceratopogonidae and the Chironomid genus *Buchonomyia* Fittkau are the only Culicomorpha that have structures readily recognizable as ventral plates, and so conclusions about the basic plan in Simuliidae are based on out-group comparison with these taxa. The ventral plate is a triangular or sub-triangular structure that arises from the ventral wall of the aedeagus; it is situated between, and dorsal to, the gonopods. During copulation the ventral plate lifts the anal lobes (= sternum 10) away from the female genital opening, and enlarges the genital chamber to receive the spermatophore (Pomerantzev 1932, Wood 1978). Primitively the ventral plate is inferred to be rather flattened dorsoventrally, such as in Ceratopogonidae, *Buchonomyia*, and *Parasimulium* (**0**). In *Prosimulium* there is a pronounced lip or emargination apicoventrally, which gives the ventral plate a distinctive triangular appearance in terminal view (**1**) (fig. 16). No other prosimuliine has such a pronounced lip on the ventral plate (figs. 17-22). Certain species of *Helodon s.str*. have a very short lip, but I have interpreted this as an independent modification of the basic plan. In Simuliini the form of the ventral plate is extremely varied, and any similarity with the ventral plate of *Prosimulium* must be attributed to parallelism. A flattened ventral plate is probably also in the groundplan of Simuliini, as inferred from the occurrence of that state in some of the most plesiotypic lineages of that tribe (*e.g. Procnephia, Paracnephia,* and *Mayacnephia*). Peterson (1970) drew attention to another distinctive feature of *Prosimulium,* which is a dorsal concavity near the base of the ventral plate. This, too, is a possible synapotypy of *Prosimulium,* but I am unable to draw any definite conclusions about the polarity of this character from out-group families. No such concavity is evident in *Parasimulium* nor any other Prosimuliini.

Character 9.

Lateral plate of prothoracic proleg broad, with vertical portion well developed. — As discussed under character 51 of chapter 2, the lateral plate of the prothoracic proleg is interpreted as a groundplan apotypy of Simuliinae. Peterson (1970) recognized 2 character states of the lateral plate in his revision of the *Prosimulium s.lat.* of Canada and Alaska: one, in which the plate is in the form af a narrow, sclerotized, horizontal bar, with little or no indication of vertical development; and another, in which the plate is a broader structure with pronounced vertical development. Out-group comparison with members of Simuliini indicates that the first mentioned condition is plesiotypic for Prosimuliini (**0**). This is the condition in Prosimuliini, exclusive of *Prosimulium s.str.* (fig. 40). A broad lateral plate with pronouced vertical development must therefore be derived, and can be taken as evidence of the monophyly of *Prosimulium* (**1**) (fig. 41).

3.6.2 Subgenus ***Helodon*** (***Helodon*** Enderlein, 1921)

HELODON Enderlein, 1921: 199. Type species: *Simulia ferruginea* Wahlberg, 1844, by original designation.

HAIMOPHAGA Rubtsov, 1977: 49 (as subgenus of *Ahaimophaga*). Type species: *Prosimulium multicaulis* Popov, 1968 (Parazitologiya 2: 444), by original designation.

AHAIMOPHAGA Chubareva & Rubtsov in Chubareva 1978: 42. Type species: *Prosimulium alpestre* Dorogostaisky, Rubtzov & Vlasenko, 1935, by original designation.

Helodon s.str. is the second largest aggregate of Prosimuliini, comprising no fewer that 18 valid species (Appendix 1). Fifteen of these species are distributed throughout the western Nearctic- (Rocky mountains from California north to Alaska, east to Baffin Island), and eastern Palaearctic- (the Soviet far east, Siberia, Japan) regions. The three other species are distributed as follows: *H. rufus* (Meigen) (Scandinavia, northwest USSR); *H. maruashvili* (Machavariani) (USSR — Transcaucasia); and *H. laamii* (Beaucournu-Saguez & Bailly-Choumara) (Morocco).

Enderlein (1921) described the genus *Helodon* by distinguishing it in a key to genera, and by designating the genotype *Simulia ferruginea* Wahlberg (= junior synonym of *Helodon rufus* (Meigen)). The couplet used to separate *Helodon* from *Prosimulium* is as follows[4]:

> Claw of female with a striking long tooth; of male much shorter
>
> *Helodon* Enderl. 1921
>
> Claw of female also simple. Hind leg of male with very long hairs
>
> *Prosimulium* Roub. 1916 (*sic*)

Enderlein did not expand upon this description in any of his subsequent works, and referred to the genus only a single additional species (*viz. Prosimulium pleurale* Malloch).

Rubtsov (1940, 1956, 1964) followed Enderlein's lead by accepting *Helodon* as a valid genus, although in a somewhat different sense. He distinguished the various life-history stages of *Helodon* as follows (Rubtsov 1964)[5]:

> Adults (males)
>
> Coloring of the body reddish. .... Genus **Helodon End.**
>
> Coloring of the body black. .... Genus **Prosimulium Roub.**

---

[4] Translated from German.

[5] Translated from German.

Adults (females)

Body color reddish. Frons narrow, its width 1/3 to 1/2 of the height.

.... Genus **Helodon** End.

Body color black. Frons broad, wider than high.

.... Genus **Prosimulium** Roub.

Larvae

Head solidly dark, with indistinct dark spots on the front.

.... Genus **Prosimulium** Roub.

Head chitin-yellow, with very distinct black spots on the front and around the base of the head. .... Genus **Helodon** End.

Pupae

Respiratory organ in the form of a thick stalk with a mass of small thin short filaments. .... Genus **Helodon** End.

The respiratory organ consists of thin filaments or tubes that are split up for different distances from the base. ...... Genus **Prosimulium** Roub.

Genus **Stegopterna** End.

Helodon, as defined above, is considerably more restricted than originally conceived by Enderlein. Indeed, if Rubtsov's generic limits were to be followed, there would be only a total of three species referable to *Helodon* world-wide (*H. rufus, H. rubicundus, H. onychodactylus*). Rubtsov evidently did not put much weight on the toothed condition of the female tarsal claw, and was instead more impressed with both the reddish color of the adult, and the unusual club-like form of the pupal respiratory organ. However, as indicated by Stone (1963), most of the characters used in Rubtsov's concept of *Helodon* are also found in various combinations in other prosimuliine species. For example, males and females of *Prosimulium* (*Prosimulium*) *fulvum* (Coquillett) are both bright orange, as are females of *P.* (*P.*) *fulvithorax* Shewell. This lack of clear-cut characters has caused most western workers to regard *Helodon* as either "a weakly defined subgenus of *Prosimulium*" (Stone 1963), or "... as forming at most a species-group within *Prosimulium s.str.* ..." (Crosskey 1969).

Peterson (1970), in his revision of the *Prosimulium s.lat.* species of Canada and Alaska, defined the subgenus *Helodon* in a sense that was less inclusive than the one proposed by Enderlein (*i.e.* not including all prosimuliine species whose females possess a toothed claw), but rather more inclusive than the one put forward by Rubtsov (*i.e.* including species whose adults are black, and whose pupal gills are not in the form of club-like structures supporting many fine filaments). Although most of the characters used to define this segregate are symplesiotypic, at least two are evidently derived, and can be taken as evidence of the monophyly of *Helodon s.str.*, as defined in the present work (see below).

Rothfels (1979) provided cytological evidence for the monophyly of *Helodon s.str.*, as defined in the present work. Chromosomal rearrangements of this segregate differ profoundly from other Prosimuliini. They exhibit both a whole arm interchange, combining IIIS and IIL, and a nucleolar organizer transposition from its standard site in *Prosimulium* (IL base) to the center of the IIL arm (*i.e.* the new IIIL) (fig. 2). Both of these cytological features are autapotypic for members of *Helodon s.str.* In addition, all members share several basic inversions that also appear in various combinations in other lineages of Prosimuliini. I can conclude only that these other inversions have developed in parallel several times.

Rubtsov (1977) proposed the new genus *Ahaimophaga* for species that were formerly placed in the "*Prosimulium alpestre* group" *sensu* Rubtsov (1964), but no type was designated from among any of the six included species. Although Rubtsov and Yankovsky (1984) attribute *Ahaimophaga* to Rubtsov and Chubareva in Rubtsov (1977), the name is clearly unavailable from that date under Arcticle 13 (b) of the International Code of Zoological Nomenclature. The subgenus *Haimophaga* was simultaneously proposed by Rubtsov (1977) for *P. multicaulis* Popov, with no description or definition other than the statement that *multicaulis* differs from other *Ahaimophaga* species by the structure of the mouthparts, which are adapted for blood feeding. The name *Ahaimophaga* is taken as available from Rubtsov's 1977 work, in accordance with Rubtsov and Yankovsky (1984) (Crosskey 1987).

Chubareva (1978) studied chromosomes of four species belonging to the "*Prosimulium alpestre* species group" *sensu* Rubtsov (1964). She concluded that one of these species, *P. multicaulis* Popov, was sufficiently similar to *Helodon rufus* to be included in the genus *Helodon*. Since *P. multicaulis* is the type species of *Haimophaga* Rubtsov (see above), this latter name is a junior subjective synonym of *Helodon* Enderlein (Crosskey 1987). The three other species studied (*P. alpestre* D. R. &V., *P. altaicum* Rubtsov, and *P. kamtshaticum* Rubtsov) were said to be intermediate between *Helodon* and *Prosimulium*, and the new genus *Ahaimophaga* Chubareva & Rubtsov in Chubareva (1978) was erected to accomodate them. However, as indicated by Rothfels (1979), members of the *alpestre* group share with *H. rufus* several cytological characteristics not shared by any other other prosimuliine, and so it is doubtful that a genus should be recognized on what are apparently minor chromosomal differences. I have followed the lead of Rothfels (1979) and Crosskey (1981, 1987) in regarding *Ahaimophaga* and *Helodon* as subjective synonyms

The immature stages of species of *Helodon* are found primarily in fast-flowing mountain streams and rivers. Larvae may be collected from a variety of substrates, but most are attached to trailing vegetation and submerged twigs. Pupae are typically attached to the sides of stones, but may also be buried deep in the stream bed (Peterson 1970, personal observation). Adult females of many species have slightly developed mouthparts, and are therefore presumed to be incapable of taking a blood meal. Females with well-developed mouthparts are presumed to be primarily ornithophilic.

Monophyly of *Helodon* (*Helodon* Enderlein)

Character 29.

Spermatheca elongate, delicate, and lightly pigmented. — As discussed under character 7 the spermatheca is a highly varied structure that has characteristic form in certain genus groups of Prosimuliini. Females of *Helodon s.str.* have a spermatheca that is typically in the the form of an elongate, delicate, lightly-pigmented sac (**1**) (fig. 11). In the Prosimuliini groundplan, the spermatheca is inferred to be a rather more rounded and densely sclerotized structure, such as found in females of *Parasimulium, Parahelodon, Urosimulium, Gymnopais* and many Simuliini (**0**) (figs. 12, 15). The spermatheca of females of *Prosimulium s.str.* is also rather delicate and lightly pigmented; however, the apex is rather more acuminate in forms that are elongate, and there is a large area of differentiated membrane at the junction with the spermathecal duct (see discussion of character 7) (fig. 10) (**1′**). Similarly, the delicate, lightly pigmented spermathecae of *Levitinia* and *Twinnia* are distinguished by their "mushroom-like" appearance, and by a large area of differentiated membrane basally (fig. 14) (**1′**). Females of *Distosimulium* have a spermatheca in the form of a greatly inflated, unpigmented bag (see character 56) (fig. 13) (**1′′**).

The elongate, delicate, lightly pigmented spermatheca appears to be unique in Prosimuliini, and can be taken as evidence of the monophyly of *Helodon s.str.* (1). The female of *Helodon susanae* (Peterson) has a rounded, delicate and lightly pigmented spermatheca. However, that species consists only of parthenogenetic females (Currie 1986), and so it is possible that the rounded condition is actually a reversal toward the primitive form.

Character 30.

Postgenal cleft biarctate, or subrectangular with faint anterior margin. — Larvae of *Helodon s.str.* are readily distinguished from those of most other Prosimuliini by the form of the postgenal cleft. This is particularly true if the comparison is restricted to Prosimuliini, exclusive of *Prosimulium s.str.* The postgenal cleft of this latter group is of greatly varied shape, and there are forms that approach the types found in *Helodon s.str.* Typically, the cleft of *Helodon s.str.* members is broader than deep, and has along its anterior margin a short, posteriorly directed, sclerotized process. The effect is a postgenal cleft that is biarctate anteriorly (fig. 33; see also fig. 55 of chapter 2). This form is clearly unique among Prosimuliini, and must be considered derivative. However, there are certain species of *Helodon* (*e.g. H. perspicuus* Sommerman), or species groups (*e.g.* certain members of the *H. onychodactylus* Dyar and Shannon complex) in which the ventrally directed process is not clearly manifest. In such instances the postgenal cleft appears to be a rather subrectangular shaped structure, but with an indefinite anterior margin.

This latter form approaches the condition found in certain species of *Prosimulium s.str.*, and so it is possible that a subrectangular-shaped cleft represents the progenitor of the biarctate form. If this were so, the biarctate condition could be used to define only groups of species within *Helodon s.str.*, and could not be construed as a synapotypy of the entire subgenus. However, cytological evidence has shown that *H. perspicuus* is clearly derived from an ancestor that had a biarctate postgenal cleft (cf. Rothfels 1979, fig. 3), and so in at least one species, a subrectangular postgenal cleft with a faint anterior margin has been derived from the biarctate condition.

As already indicated, the postgenal cleft of larvae of *Prosimulium s.str.* is extremely varied, which makes conclusions about character polarity in other Prosimuliini difficult to establish. Character states within Prosimuliini, exclusive of *Prosimulium s.str.*, are as follows: inverted U-shaped (*Distosimulium*; *Parahelodon*, 2 species; *Urosimulium*, 2 species), inverted V-shaped (*Parahelodon*, 1 species), biarctate (*Helodon* in part), subrectangular with faint anterior margin (*Helodon* in part), absent (*Levitinia, Twinnia* and *Gymnopais*). The larva of *Urosimulium faurei* has a subrectangular-shaped postgenal cleft, however, I am unable to determine from the illustration whether or not the anterior margin is indistinctly defined in that species (cf. Bernard *et al.* 1972, fig. 2a). Because the inverted U-shaped postgenal cleft is wide-spread among the in-group, and is also common in *Prosimulium s.str.* and primitive Simuliini, I have interpreted it as primitive for members of Prosimuliini, exclusive of *Prosimulium s.str.* (**0**). A cleft that is biarctate, or subrectangular with a faint anterior margin, must therefore be derived, and can be taken as evidence of the monophyly of *Helodon* s.*str.* (**1**). Other character states are as follows: (**1´**) postgenal cleft inverted V-shaped; (**1´´**) postgenal cleft rudimentary or absent.

3.6.3 Subgenus ***Helodon*** (***Parahelodon*** Peterson, 1970)

PARAHELODON Peterson, 1970: 36. Type species: *Simulium decemarticulatum* Twinn, 1936, by original designation.

The subgenus *Parahelodon* was erected for a group of three moderately distinctive species of *Prosimulium s.lat.* (Peterson 1970) : *H.* (*Ph.*) *decemarticulatus* (Twinn), *H.* (*Ph.*) *gibsoni* (Twinn), and *H.* (*Ph.*) *vernalis* (Shewell). The first two mentioned species are widespread in Canada and the northern United States; whereas the third, *H. vernalis*, occurs only in eastern Canada and the northeastern United States. Most of the characters used to define this segregate are symplesiotypic, and cannot be used to demonstrate phylogenetic relationships. However, the four apotypic characters enumerated below provide strong evidence of the monophyly of the subgenus, as defined by Peterson.

Rothfels (1979), in his cytological transformation series of species derived from *Helodon s.lat.*, listed inversion "1 x IIS" as a constitutive feature of the three nominal species belonging to *Parahelodon*[6]. Cytological information was also used to provided evidence of a sister-group relationship between *H. vernalis* and *H. decemarticulatus* + *H. gibsoni*. These three species together were placed as the sister group of *H.* (*Distosimulium*) *pleuralis*, and this entire assemblage was placed as the sister group of *Helodon s.str.* (cf. Rothfels 1979, fig. 3). Phylogenetic relationships among the 3 included species of *H.* (*Parahelodon*) are diagrammed in figure 4.

Novák (1957) referred *H. gibsoni* to the genus *Twinnia*, based on similarities of the pupa (both *H. gibsoni* and *T. hydroides* (Novák) have a 14-filamented gill) and adult (7-articled flagellum of antenna; features of the male terminalia). However, he was evidently not aware that the larva of *H. gibsoni* possesses fully-developed labral fans. *Twinnia* belongs to a monophyletic group of Prosimuliini (including *Levitinia* and *Gymnopais*) whose larvae lack labral fans.

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[6] Rothfels (1979) indicates that *H. decemarticulatus* and *H. gibsoni* each consist of two cytologically distinct cytospecies.

The three species of *Parahelodon* are all rather similar ecologically. The immature stages typically live in small, first- or second-order streams, such as springs, bogs seeps, drainage ditches, or outflows from beaver ponds (Sommerman *et al.* 1955, Peterson and Wolfe 1958, Anderson and Dicke 1960, Peterson 1970, Currie 1986). Adult females of two species have been recorded as blood feeders upon birds (*H. decemarticulatus*, *H. vernalis*); females of *H. gibsoni* have slightly developed mouthparts, and therefore are presumed to be incapable of blood feeding (Peterson 1970).

Monophyly of the subgenus *Parahelodon*.

Character 51.

Arm of genital fork (= sternum 9) bearing a typically wrinkled or denticulate pronounced terminal plate. — In characterizing females of *Parahelodon,* Peterson (1970) remarked about the large, slightly sclerotized plate (= terminal plate) that arises apically from each arm of the genital fork. Not only is the plate relatively large in comparison with those of most other Prosimuliini, but it is typically wrinkled or denticulate (**1**) (fig. 12). No such wrinkling or denticulation is evident on the termininal plates of other Prosimuliini females (**0**) (figs. 10, 11, 13-15). The terminal plate of *Prosimulium s.str.* is rather varied in form, but any similarity with that of *Parahelodon* is strictly due to convergence. The terminal plate of *Distosimulium* females is even larger than that of *Parahelodon*; however, the cuticle of that plate is neither wrinkled, nor denticulated (fig. 13). A large terminal plate is interpreted as a groundplan apotypy of *H.* (*Parahelodon*) + *H.* (*Distosimulium*) (see also discussion of characters 31 and 55).

Character 52.

Ventral plate of aedeagus with digitiform dorsomedial projection basally, to which base of median sclerite is fused. — Males of *Parahelodon* are unique among Simuliidae in having the anterodorsal surface of the ventral plate produced finger-like distinctly beyond the apices of the anterolateral apodemes (**1**) (fig 18). This projection gives rise to the median sclerite, which projects posterodorsally to serve as a mid-ventral support for the aedeagus. In other Simuliidae, the anterodorsal surface of ventral plate is not produced finger-like beyond the apices of the anterolateral apodemes, and the median sclerite has, at most, a short rounded base (**0**) (figs. 16, 17, 20-22).

Character 53.

Ventral plate of aedeagus with anterolateral apodeme short. — The anterolateral corner of the simuliid ventral plate is produced into an arm-like apodeme that connects with the gonocoxite and/or paramere. Typically, the "anterolateral apodeme" (or "arm") is relatively long and broad, and comprises a substantial proportion of the total length of the ventral plate. Such a condition is found in males of *Prosimulium, Helodon, Distosimulium, Urosimulium, Twinnia,* and *Gymnopais* (figs. 16, 17, 20-22). Males of *Levitinia* have an anterolateral apodeme that is comparatively short relative to the total length of the ventral plate, although broad and conspicuous. In *Parahelodon* males the anterolateral apodeme is shorter yet, and rather slender (fig. 18). Out-group comparison with *Parasimulium* and Simuliini indicates that the long-armed condition is probably in the groundplan of Prosimuliini (**0**), and that a short, slender, arm is a secondary development (**1**). The short-armed condition in *Parahelodon* and *Levitinia* has probably been derived independently, as judged from other characters.

Character 54.

Gonostylus with single, peg-like seta apically. — Males of *Parahelodon* are distinguished from males of most other Prosimuliini by a single, peg-like, seta near the apex of the gonostylus. The number of apical setae in other genus groups is as follows: *Prosimulium s.str.* (2-6, rarely 1), *Helodon s.str.* (2-5), *Distosimulium* (3), *Urosimulium* (2), *Levitinia* (2), *Twinnia* (1, rarely 2), and *Gymnopais* (1-3). Although the number of apical setae is varied in *Prosimulium* and *Helodon*, it is clear that 2 is the most commonly encountered condition. I have interpreted 2 apical setae as the groundplan number for Prosimuliini (**0**) (figs. 16, 17, 19, 22). Presence of only 1 seta must therefore be a loss, and is evidence of the monophyly of *Parahelodon* (**1**) (fig. 18). However, the gonostyli of males of *Twinnia* , *Gymnopais* (in part), and *Prosimulium unispinum* Rubtsov also only have a single seta apically. Because of homoplasy, the derived state can only be considered a weak phylogenetic indicator.

3.6.4 Subgenus ***Helodon*** (***Distosimulium*** Peterson, 1970)

DISTOSIMULIUM Peterson, 1970, *Memoirs of the Entomological Society of Canada* **69**: 30. Type species: *Prosimulium pleurale* Malloch, by original designation.

The taxon *Distosimulium* was erected (as a subgenus of *Prosimulium* Roubaud) by Peterson (1970) to accomodate *Prosimulium pleurale* Malloch. This species is distributed throughout Alaska, eastern and western Canada, and the northwestern United States. According to Rothfels (1979) the eastern and western populations of *H. pleuralis* may represent two cytologically distinct sibling species. Uemoto *et al.* (1976) referred to *Distosimulium* a second species, *Prosimulium daisetsense* Uemoto, Okazawa & Onishi, from Hokkaido, Japan. This necessitated a rediagnosis of *Distosimulium*, for several of the characteristics listed in the original description have proven to be autapotypic for *Helodon pleuralis*, the type species (Uemoto *et al*. 1976).

The phylogenetic relationships of *Distosimulium* are reasonably clearly established. In erecting the subgenus, Peterson (1970) indicated that *H. pleuralis* is more closely related to species of *Helodon s.str.* and *Parahelodon* than it is to species of *Prosimulium s.str.* However, the structural attributes of this species appeared distinctive enough to warrant subgeneric recognition. Uemoto *et al*. (1976) indicated that *H. daisetsensis* is phylogenetically intermediate between *Distosimulium* and *Parahelodon*, but relegated the species to the former subgenus based mainly on similarities of the male and female terminalia. Rothfels (1979), in his chromosome transformation series of species derived from "*Helodon* standard", chose not to recognize the subgenus *Distosimulium*, and instead relegated *H. pleuralis*, along with species of *Parahelodon*, to "*Helodon s.lat.*" *Helodon pleuralis* was considered the sister taxon of *vernalis* + *decemarticulatus* + *gibsoni* (= *Parahelodon sensu* Peterson 1970), and this entire assemblage was placed as the sister group of all other *Helodon* (= *Helodon s.str.*) (fig. 2).

Very little is known about the natural history of *Distosimulium* species. Immatures are frequently encoutered in mountain- or bog drainage-type streams with rocky bottoms (Jenkins 1948, Peterson 1970, Uemoto *et al*. 1976). Shewell (1957) reported that females of *H. pleuralis* are occasional or localized pests of man and domestic mammals, although it is more likely that they blood feed upon birds (Peterson 1970).

Monophyly of the subgenus *Distosimulium*.

Character 55.

Arm of genital fork (sternum 9) with a markedly pronounced terminal plate that bears a patch of setae. — As already discussed under character 51, females of *Parahelodon* and *Distosimulium* are both distinguished by the relatively large terminal plate. The terminal plate of *Distosimulium* is so large that its posterior margin projects conspicuously beyond the posterior margin of the hypogynial valves (= posterior margin of sternum 8) (fig. 13) The condition in other Prosimuliini is for the posterior margin of the terminal plate to either project slightly beyond the posterior margin of the hypogynial valves (*Parahelodon*; fig. 12), or be completely overlain by the valves (all remaining genus groups; figs. 10, 11,14, 15). Although I have interpreted a large terminal plate as a groundplan apotypy of *Parahelodon* + *Distosimulium* (character 31), it is clear that the exceptionally large size of that structure in *Distosimulium* females is a further derived state. Another distinctive feature of the *Distosimulium* terminal plate is the patch of long setae that is situated centrally. No other prosimuliine that I am aware of has such pronounced setation on the terminal plate (**0**)[7]. The combination of a markedly pronounced terminal plate with a central patch of setae is taken as evidence of the monophyly of *Distosimulium* (**1**).

Character 56.

Spermatheca a greatly enlarged, thin, delicate, unpigmented bag. — The spermathecae of females of *Distosimulium* are distinguished from those of all other female Simuliidae by their extremely large size and lack of pigmentation (**1**) (fig. 13). The spermatheca is so large and delicate that it is difficult to see in many specimens, and therefore may appear to be absent (Peterson 1981). No other simuliid has a spermatheca that is so large or completely unsclerotized (**0**) (figs. 10-12, 14, 15). The spermathecae of some taxa are characterized by a variably sized area of unsclerotized, differentiated membrane at the junction with the spermathecal duct, but these are invariably pigmented or patterned apically (*e.g.* fig. 10).

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[7] A few scattered setae are found on the terminal plates of some females of *Twinnia* (in part) and *Gymnopais fimbriatus* Wood.

Character 57.

Ventral plate of aedeagus deeply cleft apically. — The ventral plate of males of *Distosimulium* are unique among Prosimuliini in having the posterior margin deeply cleft. Coupled with the relatively long anterolateral arms of the ventral plate, the entire structure appears to be rather H-shaped in ventral view (**1**) (fig. 20). The ventral plates of other Prosimuliini are neither deeply cleft nor H-shaped in ventral view, and are at most only shallowly emarginated apically (**0**) (figs. 17, 18, 21, 22). The only other simuliid that I am aware of that has an H-shaped ventral plate are males of *Simulium* subgenus *Shewellomyia*; however, this would have to be interpreted as an independent development, as judged from other characters.

Character 58.

Gonostylus with apical half markedly thinner than proximal half, tapered posteriorly to an acute point. — In the prosimuliine groundplan, the gonostylus appears to be a rather evenly tapered structure in ventral view. Further, the gonostylus is typically narrowly- to broadly-rounded apically. This is the condition found in members of *Helodon, Parahelodon, Urosimulium, Levitinia, Twinnia,* and most *Prosimulium* (**0**) (figs. 16-18, 21). The gonostylus of males of *Distosimulium* differs from those of most other Prosimuliini in that the apical half is markedly thinner than the proximal half in ventral view, and the apex is tapered to an acute point (**1**) (fig. 20). Males of *Gymnopais* Stone are the only other prosimuliines with the gonostylus markedly tapered near the apex, although this would have to be considered an independent development (fig. 22) (see also discussion of character 78).

Character 59.

Gonostylus flexed in dorsoventral plane, its apex opposed to spiniform, dorsoventrally curved paramere. — Wood and Borkent (1982) remarked on the mode of action of the gonostylus of of *Helodon pleuralis*. In the nematoceran groundplan the gonocoxites are diverged laterally, and the gonostyli oppose each other apically in a lateromedial plane. This is the condition of most male simuliids (**0**) (figs. 16-18, 21, 22). The gonostyli of males of ***Distosimulium*** do not oppose each other medially, and instead are flexed in a dorsoventral plane (fig. 20). When fully flexed the gonostylus is opposed to the apex of the paramere, which is in the form of a dorsoventrally curved spine-like structure fused to the gonocoxal apodeme (fig. 19). In effect, the gonostylus and paramere act as a set of pincers, which evidently impinge on the enlarged terminal plate of the female genital fork (see discussion of character 55 above). Both the mode of action of the gonostylus, and the form of the paramere, are taken as strong evidence of [illegible] monophyly of ***Distosimulium*** (**1**). The only other simuliids with a similar arrangement are males of ***Parasimulium***; however, the dorsoventrally flexed gonostyli are opposed to the apicolateral angle of the ventral plate, and not the paramere (Wood and Borkent *loc. cit.*). The condition in ***Parasimulium*** is therefore considered to be an independent development.

Character 60.

Postgenal cleft of larva deep and broad. — Larvae of *Distosimulium* have the most extensive postgenal cleft of any larval prosimuliine. It is relatively broad and inverted U-shaped, and is extended from one-third to one-half the distance from the posterior tentorial pits to the hypostomal groove (fig. 32). The form of the postgenal cleft is rather varied in other larval Prosimuliini, but is extended in few taxa farther than about one-quarter the distance from the posterior tentorial pits to the hypostomal groove (figs. 30, 31, 33, 34). A shallow postgenal cleft is probably in the groundplan of Prosimuliini, as judged from the distribution of this character state throughout the tribe (0) (see also discussion of character 30). A deep and broad cleft must therefore be derived, and is evidence of the monophyly of *Distosimulium* (1).

3.6.5 Genus *UROSIMULIUM* Contini, 1963

UROSIMULIUM Contini, 1963: 89. Type species: *Urosimulium stefanii* Contini, 1963 [=*Urosimulium aculeatum* (Rivossecchi), 1963], by original designation.

The genus *Urosimlium* Contini is comprised of three species that have a western Mediterranean distribution (Morocco, Sardinia, Sicily). *Urosimulium aculeatum* (Rivossecchi) and *U. juccii* Contini are the only two species so far assigned to this segregate. The third species, *U. faurei* (Bernard, Grenier & Bailly-Choumara 1972), has previously been assigned to *Prosimulium s.str.*, but shares with the other two species all the synapotypies listed below for *Urosimulium*. It is here relegated, in new combination, to this latter genus.

The relationship of *Urosimulium* to other Prosimuliini has not been clearly established. Some authors regard this aggregate as a distinct genus (Contini 1963, 1966; Rubtsov 1974; Rivosecchi 1978); whereas others regard it as no more than a moderately distinctive species group of *Prosimulium s.str.* (*i.e.* the *aculeatum* group) (Crosskey 1969, 1981, 1987; Bernard *et al.* 1972). Rothfels (1979) provided support for this latter view by suggesting that *U. stefanii* Contini (= *aculeatum*) might belong cytologically to the *hirtipes* group of *Prosimulium s.str*. However, members of *Urosimulium* lack any of the syapotypies used to define *Prosimulium*, and instead have the single synapotypy (a bifid female claw) used to define the sister group of *Prosimulium*. Until the relationships of *Urosimulium* are better understood, I prefer to recognize this segregate as a full genus. Phylogenetic relationships among the 3 included species are diagrammed in figure 5.

Very little is known about the natural history of *Urosimulium* species. The immature stages typically live in small- to large-sized mountian streams (Rivosecchi 1963, Bernard *et al.* 1972). Mature larvae may be found in March, with adult emergence period extending from the end of that month to mid-April. Adult females of *U. aculeatum* and *U. faurei* are probably blood-feeders, as judged from the toothed condition of their mandibles and maxillary lacinia. Nothing is known about their hosts. The female of *U. juccii* is probably autogenous (Contini 1966)

Monophyly of the genus *Urosimulium* Contini.

Character 14.

Cercus of female elongate, produced apically to a fine point. — The cercus of females of *Urosimulium* is much longer than wide, and is tapered apically to a fine, posterodorsally directed point. In lateral view the cercus appears to be rather scimitar-shaped. This condition is evidently unique to females of *Urosimulium,* and provides strong evidence of the monophyly of the three included species (**1**). Females of all other Prosimuliini examined have a cercus that is broader than long, and appears subrectangular- or subquadrate-shaped in lateral view (figs. 10-15). Out-group comparison with *Parasimulium* and Simuliini indicates that a subrectangular-shaped female cercus is probably basic to Prosimuliini (**0**).

Character 15.

Gonostylus with an accessory lobe laterally at base. — This condition must not be confused with the "inner gonostylus" of many other Chironimoidea (Wood and Borkent 1982, Borkent and Forster 1986, Cranston *et al.* 1987). The inner gonostylus is an articulated appendage situated on the dorsomedial surface of the gonopod between the gonostylus and the gonocoxite. Members of *Parasimulium s.str.* are the only Simuliidae known to have such a structure. A similarly positioned (but probably non-homologous) structure is present in certain members of *Simulium s.str.*, which have a non-articulated, spinose, lobe lateromedially on the base of the gonostylus. The condition in males of *Urosimulium* differs from those described above in that the accessory lobe is a non-articulated appendage positioned laterally at the base of the gonostylus. No other simuliid that I am aware of has such a condition, which must be considered apotypic (**1**). The groundplan condition for Prosimuliini is for a simple gonostylus (**0**) (figs. 16-22).

Character 16.

Larval antenna with proximal and medial articles pigmented. — As discussed under character 53 of the second chapter, the basal two articles of the larval antenna are presumed to be colorless in the Prosimuliini groundplan (**0**) (cf. fig. 58 of chapter 2). This condition is found in members of the following genera: *Prosimulium*, *Helodon s.lat.*, *Twinnia*, and *Gymnopais* (figs.30-34). The three included species of *Urosimulium* have a larval antenna that is pigmented basally, which approaches the presumed primitive condition for Simuliidae. However, the distal antennal article is markedly darker than the basal two articles, and so it seems possible that the pigmentation is actually a reversal toward the primitive form (**1**). The larva of *Levitinia* has a similarly colored antenna, but other characters suggest that this must be an independent derivation from the primitive form.

3.6.6 Genus *LEVITINIA* Chubareva & Petrova, 1981

LEVITINIA Chubareva & Petrova, 1981: 898. Type species: *Levitinia tacobi* Chubareva & Petrova, 1981, by original designation.

The genus *Levitinia* Chubareva & Petrova, 1981, was recognized for a new species (*tacobi*) of "fanless" black flies, and placed along with *Twinnia* Stone & Jamnback and *Gymnopais* Stone in the subfamily Gymnopaidinae. The description was based on a series of larvae collected from the mountains (Hissar Range) of the Tadzhikistan Republic, USSR. The features listed as diagnostic for the genus included the 5-branched anal sclerite (as compared to 3-branched in *Twinnia* and *Gymnopais*) and the 10-branched respiratory organ (as compared to 14- or 16-branched in *Twinnia*, and 6 or less branched in *Gymnopais*). Karyotypical features of the larva confirmed that *Levitinia* shared a close relationship with the other two mentioned genera, but evidently did not reveal how the three taxa were related to each other. On the basis of external structural characters (esp. the form of the larval mandible), *Levitinia* was said to occupy a phylogenetically intermediate position between *Gymnopais* and *Twinnia*.

Beaucournu-Saguez and Braverman (1987) described larvae, pupae and adults of a second species of *Levitinia* (*L. freidbergi* Beaucournu-Saguez & Braverman), from the Golan Heights, Israel. In recognizing the similarity between adults of *Levitinia* and *Prosimulium* Roubaud, and the overall close relationship between the first mentioned genus and *Twinnia* and *Gymnopais*, these authors preferred not to recognize the subfamily Gymnopaidinae, and instead relegated the fanless simuliids to the tribe Prosimuliini *sensu* Crosskey (1969, 1981, 1987). They compared the various life-history stages of *Levitinia* with *Gymnopais*, *Twinnia*, and *Prosimulium s.lat.*, but did not arrive at any definite conclusions about interrelationships among these genera.

Larvae of both species were collected from small-sized mountain streams. The habitat is characterized by high altitude and low temperature, and is climatically similar to the habitat of other Prosimuliini (Beaucournu-Saguez & Braverman 1987). Nothing is known about the natural history of adults. Adult females of *L. freidbergi* have markedly developed mouthparts, and are presumably capable of taking a blood meal. The bifid tarsal claw of the female suggests that it may be a blood feeder upon birds.

Monophyly of the genus *Levitinia* Chubareva & Petrova.

Character 35.

Tergum 9 of female elongate posteriorly, projected shield-like over cercus. — The female of *Levitinia* can be distinguished immediately from those of all other Prosimuliini by the form of tergum 9. The posterior margin is produced posteriorly as a dart-like structure that projects well beyond the apex of the cercus. The apex of the tergum is tapered to a fine point, and the overall appearance is that of a shield (**1**). Tergum 9 of females of all other Prosimuliini is a triangular- or subtriangular-shaped sclerite that is not produced shield-like over the cerci, and the apex is narrowly to broadly pointed. This latter condition is clearly plesiotypic (**0**) (figs. 10-15).

Character 36.

Terminal plate of genital fork (= sternum 9) not connected directly to tergum 9. — The terminal plate of the genital fork of *Levitinia* females is not directly connected with tergum 9. Instead, the tergum and sternum of that segment are distinctly separated by membrane. The only other simuliid that I am aware of with a similar condition is

Gymnopais (fig. 15). A membranous connection between the tergum and sternum of segment 9 is clearly derived with respect to other simuliids, which typically have a distinct sclerotized connection between these two sclerites (figs. 10-14). Although it might be argued that the apotypic state is evidence of the immediate common ancestory of *Levitinia* and *Gymnopais*, evidence presented later suggests that *Levitinia* is the sister taxon of *Twinnia* + *Gymnopais*. There are two possible interpretations: either the lack of a connection is a groundplan feature of the fanless prosimuliines, with subsequent reversal to the primitive form in *Twinnia*; or there has been two independent derivations of the apotypic state — once in *Gymnopais*, and once in *Levitinia*. The latter hypothesis is favored in this instance because loss of a connection is an easier step developmentally. The apotypic state is (**1**), the plesiotypic state, which is for a sclerotized connection to be present, is (**0**).

Character 37.

Ventral plate of aedeagus with anterolateral arms short. — The anterolateral corner of the simuliid ventral plate is produced into an arm-like apodeme that connects with the gonocoxite and/or paramere. Typically, the "anterolateral apodeme" (or "arm") is relatively long and broad, and comprises a substantial proportion of the total length of the ventral plate. Such a condition is found in males of *Prosimulium, Helodon s.str., Distosimulium, Urosimulium, Twinnia,* and *Gymnopais* (figs. 16, 17, 20-22). Males of *Levitinia* have an arm comparatively short relative to the total length of the ventral plate, although broad and conspicuous. In males of *Parahelodon* the arm is shorter yet, and rather slender (fig. 18). Out-group comparison with *Parasimulium* and Simuliini indicates that the long-armed condition is in the groundplan of Prosimuliini (**0**), and that a short, slender, arm is a secondary development (**1**). The short-armed condition in *Parahelodon* and *Levitinia* has probably been derived independently, as judged from other characters.

Character 38.

Paramere rudimentary, not connected to anterolateral apodeme of ventral plate. — The paramere of male Simuliidae is typically a large subtriangular- or subquadrate-shaped plate-like sclerite situated on either side of the aedeagal membrane. As discussed under character 60 of chapter 2, the paramere is primitively connected with both the anterolateral apodeme of the ventral plate and the anterodorsal margin of the gonocoxite (= gonocoxal apodeme) (figs. 16, 17). In males of *Levitinia, Parahelodon,* and *Distosimulium* the "strap-like connection" between the paramere and the anterolateral apodeme evidently has become lost, and the paramere remains articulated only with the gonocoxal apodeme (figs. 18-20). This condition, which is clearly derivative, has evidently been evolved a number of times independently in Simuliidae, and at least twice in Prosimuliini: once in *Levitinia,* and once in *Parahelodon* + *Distosimulium* (see also discussion of character 33). The paramere of *Levitinia* is further derived in that it is in the form of a fine, finger-like projection fused to the gonocoxal apodeme (**1**). Indeed, there is no clear separation between the paramere and the gonocoxal apodeme where the two structures are joined together. No other Prosimuliini has such an ill-formed paramere, and the connection with the gonocoxal apodeme is typically rather tenuous (**0**). The paramere of *Distosimulium* is fused to the gonocoxal apodeme, but the distal portion of that structure is produced into a long, strongly sclerotized spine that curves ventrally to oppose the apex of the gonostylus (see discussion of character 59).

Character 39.

Pupal abdomen without a pleurite on segment 4, segment 3 with wide tract of pleural membrane. — Presence of a large pleurite on each of pupal abdominal segments 4 and 5 has been interpreted as a groundplan apotypy of Prosimuliini (see discussion of character 52 in chapter 2). Such a condition is found in each the following lineages: *Prosimulium, Helodon s.str., Parahelodon, Distosimulium, Urosimulium,* and *Twinnia* (figs. 6a, 6c). The pupa of *Levitinia* has a large pleurite on abdominal segment 5, but not on segment 4 (fig. 6b). Although this lesser number of pleurites could be construed as an intermediate stage of a transformation series between the condition found in Simuliini (in which pleurites are small or absent on segments 4 and 5), and that found in most other Prosimuliini, it seems more likely that the pleurite has simply become lost from segment 4 of *Levitinia*. As will be discussed later, *Levitinia* is hypothesized to be the sister taxon of *Twinnia* and *Gymnopais* together, and so if the condition in *Levitinia* is truely primitive for Prosimuliini, then the large pleurite on segment 4 would have to have been evolved at least twice: once in the *Twinnia* — *Gymnopais* line, and once in all other Prosimuliini. The first mentioned hypothesis seems simpler, and is accepted here.

Another unique (for Prosimuliini) feature of the pupal abdomen of *Levitinia* is the relatively wide tract of pleural membrane that separates the tergum and sternum of segment 3 (fig. 6b). In other Prosimuliini, the tergum and sternum are either separated by a narrow tract of pleural membrane (*Prosimulium, Helodon s.str., Parahelodon, Distosimulium* and *Urosimulium*) (fig. 6a) or are fused together to form a ring-like structure (*Twinnia* and *Gymnopais*) (figs. 6c, 6d). The narrowly separated condition between the tergum and sternum on segment 3 of most Prosimuliini seems to be derived from a large pleural plate that has become fused ventrally with the adjacent sternum. The remaining narrow tract of membrane seems similar in all respects to the membrane that separates terga 4 and 5 from thier respective pleurites. The distribution of this character state suggests that it is basic to Prosimuliini (0). In *Twinnia* and *Gymnopais* pupae, the ring-like appearance of abdominal segment 3 is probably derived through fusion of both the dorsal and ventral surfaces of the pleurite with the adjacent tergum and sternum (see discussion of character 46). Hence, a ring-like segment 3 is an easy step developmentally from the Prosimuliini groundplan. The wide tract of membrane between tergum and sternum 3 of *Levitinia* appears to be an independent derivation of the basic plan, perhaps through loss of the pleurite.

In summary, the wide tract of pleural membane on pupal abdominal segments 3 and 4 of *Levitinia* is attributed to loss of their respective pleurites (1). The evolutionary significance of this arrangement cannot be determined until more is learned about the natural history of pupae of *Levitinia*.

Character 40.

Larval antenna with proximal and medial articles pigmented. — As discussed under character 53 of the second chapter, the basal two articles of the larval antenna are presumed to be colorless in the Prosimuliini groundplan (0). This condition is in members of the following genera: *Prosimulium, Helodon s.lat., Twinnia,* and *Gymnopais*. In the two included species of *Levitinia,* the larval antenna is pigmented basally, which approaches the presumed primitive condition for Simuliidae. However, the distal antennal article is markedly darker than the basal two aricles, and so it seems possible that the pigmentation is actually a reversal toward the primitive form (1). The antenna is otherwise similar to the ones found in most other Prosimuliini. Larvae of *Urosimulium* also have the basal two articles of the antenna pigmented, but other characters suggest that this has been derived independently from the primitive form.

Character 41.

Hypostoma of larva with lateral serrations produced as spiniform setae. — Currie (1986) reviewed terms used to describe the larval hypostoma of Simuliidae. The term "lateral serrations" was applied to the denticulations that lie lateral to the apical hypostomal teeth. Unlike "apical teeth", which are typically darkly sclerotized and derived from the dorsal wall of the hypostoma, lateral serrations are relatively slightly sclerotized and are derived from the ventral wall of the hypostoma. Larvae of *Levitinia* are evidently unique among Simuliidae in that the lateral serrations are in the form of elongate, spiniform seta

(**1**). The typical condition for Simuliidae is for the lateral serrations to be in form of short, broadly- to narrowly-rounded denticulations (**0**).

Character 42.

Anal sclerite with a prominent supernumerary arm projected posteromedially from the median sclerite, resulting in an inverted-star shaped structure. — In the Prosimuliini groundplan, the anal sclerite is hypothesized to consist of a median sclerite and 4 radiating arms — 2 anterodorsal and 2 posteroventral (fig. 9a). This condition is characteristic of the following genus groups: *Prosimulium*, *Helodon s.str.*, *Parahelodon*, and *Distosimulium*. The same basic pattern can be seen in the anal sclerites of other genus groups as well (*Urosimulium*, *Levitinia*, *Twinnia*, and *Gymnopais*), except that there is an additional projection arising posteromedially from the area between the posteroventral arms (figs. 9b-9c). I suggested in the discussion of character 13 that a short posteromedially directed projection, such as in *Urosimulium* (fig. 9b), might represent the groundplan condition for *Urosimulium* + the fanless Prosimuliini. The anal sclerite of *Levitinia* seems further derived in that the projection is in the form of a prominent arm, subequal in proportion to the anterodorsal and posteroventral arms. The resulting "inverted-star" shaped anal sclerite is unique among Simuliidae, and is strong evidence of the monophyly of *Levitinia* (**1**). The primitive condition is for the anal sclerite to be X-shaped, or X-shaped with only a short, posteromedially directed projection (**0**).

3.6.7 Genus *TWINNIA* Stone & Jamnback, 1955

TWINNIA Stone & Jamnback, 1955: 18. Type species: *Twinnia tibblesi* Stone & Jamnback, 1955, by original designation.

The nominal taxon *Twinnia* Stone & Jamnback, 1955, was recognized for two species (*tibblesi*, *nova*) whose adults appeared to be closely related to *Prosimulium* Roubaud, but whose fanless larvae suggested a close relationship with *Gymnopais* Stone. *Twinnia* was considered distinctive enough to rank at the generic level, and was placed along with *Gymnopais*, *Prosimulium*, and *Cnephia* in the subfamily Prosimuliinae.

Shewell (1958) accepted *Gymnopais* as a separate genus of Prosimuliinae, but preferred to rank *Twinnia* as a subgenus of *Prosimulium*. He pointed to the apparent lack of differences between the adults and pupae of these latter two segregates as justification for this action. Rubtsov (1964), on the other hand, rejected the hypothesis of a close relationship between *Twinnia* and *Prosimulium*, and relegated the former genus to the subfamily Gymnopaidinae. This subfamily was originally proposed monobasic for *Gymnopais*, based on the assumption that the fanless condition is primitive for Simuliidae (Rubtsov 1955, 1974).

Craig (1974) and Wood (1978) provided convincing evidence that the fanless condition is in fact secondary, and that *Twinnia* and *Gymnopais* share an immediate common ancestor with *Prosimulium s.lat*. This interpretation is supported by cytological evidence, which shows that *Twinnia* and *Gymnopais* are clearly derived from the *Prosimulium* "standard" sequence (Rothfels and Freeman 1966; Rothfels 1979).

The ten described species of *Twinnia* are distributed throughout the temperate forests of the Holarctic region. *Twinnia hydroides* (Novák) and *T. tatrensis* Novák occur in Europe; *T. sedecimfistulata* (Rubtsov) and *T. magadensis* Rubtsov in Siberia; *T. japonensis* Rubtsov, *T. cannibora* Ono, and *T. subtibbelesi* [*sic*] Ono in Japan; *T. nova* (Dyar & Shannon) and *T. hirticornis* Wood in western North America; and *T. tibblesi* Stone & Jamnback in eastern North America.

The immature stages of *Twinnia* are typically either in the headwaters of small, spring-fed streams, or in streams that simulate this type of habitat, such as outflows from impoundments (Wood 1978, personal observation). Adult females have been reported as either autogenous (Wood 1978, Zwick 1987), or anautogenous on ungulates and humans (Wood 1978, Currie 1986, Sasaki *et al.* 1986).

Monophyly of the genus *Twinnia* Stone & Jamnback

Character 61.

Body of ventral plate of aedeagus strongly emarginated laterally near base of anterolateral apodeme. — Males of *Twinnia* are distinguished from those of most other Prosimuliini by the form of the ventral plate. In ventral view the body of the plate is rather broad posteriorly, and is excavated laterally near the base of the anterolateral apodeme. This lateral emargination is magnified even farther by the fact that the anterolateral apodemes are divergent from each other apically (fig. 21). The form of the ventral plate is rather varied in other Prosimuliini, but is typically not excavated laterally near the base of the anterolateral apodeme (figs. 16-18, 20, 22). In species that have a laterally emarginate ventral plate, the anterolateral apodemes are not markedly divergent apically. Out-group comparison with *Parasimulium* and primitive Simuliini indicates that a laterally emarginated ventral plate is apotypic (1), and is taken as evidence of the monophyly of *Twinnia*. The presumed primitive condition in Prosimuliini is for the ventral plate to be more or less parallel-sided laterally, and for the anterolateral apodemes to project parallel to each other (**0**).

Character 62.

Gonostylus with a single, peg-like seta apically. — As already discussed under character 54, the groundplan number of apical peg-like seta on the gonostylus is presumed to be 2 (**0**) (figs. 16, 17, 19, 22). The gonostylus of males of *Twinnia* is characterized by the presence of a single, large, peg-like seta near the apex, which must be considered derivative (**1**) (fig. 21). The only exception to this rule is the occasional rare specimen of *T. hirticornis*, which has 2 apical setae (Wood 1978). However, *T. hirticornis* is a relatively derived species of *Twinnia*, and the majority of specimens examined have only a single apical seta. It seems possible therefore that the occasional extra seta is a reversal toward the primitive condition. The derived state also defines members of *Helodon* (*Parahelodon*) (fig. 18). Because the apotypic state is regressive and subject to homoplasy, it cannot be taken as strong evidence of the monophyly of *Twinnia*.

Character 63.

Mandible of larva not markedly curved medially near apex. — The simuliid larval mandible is typically markedly curved distally, with the apical mandibular teeth directed toward the midline of the larva (fig. 36). During adduction, the mandibular teeth interdigitate with the apical hypostomal teeth, thus forming a functional complex. Currie and Craig (1987) have suggested that this co-adaptation between the mandibular and hypostomal teeth serves as a "pan and broom" arrangement for transfer of food into the cibarium, with hairs on the anteroventral surface of the mandible (= apical mandibular brush) serving as the "broom" (cf. fig. 27, chapter 2). The larval mandible of *Twinnia* differs from this general plan in that its apex is not markedly curved toward the midline, and is instead more in line with the longitudinal axis of the mandible (1) (fig. 35). The consequence of this arrangement is that the anteroventral surface of the mandible (and hence the apical brush) is not brought into contact with the substrate during browsing. Hence, the apical mandibular teeth evidently act alone in the transfer of food into the cibarium. A markedly curved mandible is characteristic of all Prosimuliini larvae (0).

Character 64.

Mandible of larva with spine-like scales on anteroventral surface of mandible reduced. — The apical mandibular brush of *Twinnia* larvae consists of 3 or 4 rows of slender, short, bristle-like setae. This is similar to the condition of most other prosimuliine larvae, except that the brush typically consists of longer, finer hairs (cf. fig. 27, chapter 2). In addition to these hair-like setae, there are an additional three or four spine-like setae situated immediately basad of the apical mandibular teeth (Chance 1970, cf. fig. 46; Ono 1977, cf. fig. 24; Ono 1980, cf. fig. 27; personal observation). These spines are similar to the spine-like scales (= apical mandibular brush) on the anteroventral surface of the larval mandibles of *Levitinia* and *Gymnopais*, except that the scales in these two segregates are organized into 7 - 12 rows. Other evidence suggests that *Levitinia* is the sister taxon of *Twinnia* + *Gymnopais*. If the hypothesized set of relationships is accepted, then the form of the apical mandibular brush of *Twinnia* must be interpreted as a reduction or loss. As indicated under character 63 above, the anteroventral surface of the *Twinnia* mandible is probably not brought into contact with the substrate during browsing, and so it seems possible that the rudimentary nature of apical brush is indeed the result of loss. This is the interpretation followed in the present work. Character states are coded as follows: (0) apical brush consisting of hair-like or bristle-like setae; (1) apical brush consisting of 7-12 rows of spine-like setae; (2) apical brush with spine-like setae reduced to a single row of 3 or 4 spines.

Character 65.

Pupal cocoon a transparent gelatinous envelope that encloses all of pupa, retaining larval exuviae. — In the prosimuliine groundplan, the cocoon is in the form of thin- to thickly-woven silken sac covering all of the pupal abdomen, and typically most of the thorax. The cocoon is spun by the pharate pupa, and at ecdysis the larval exuviae is temporarily held between the pupal gills (= respiratory organ). However, the anterior portion of the cocoon sloughs off shortly after pupation, and the larval exuviae is typically swept away by the current. The pupal cocoon of *Twinnia* differs from this general plan in two major respects. First, it is in the form of a transparent, gelatinous, envelope that covers all of the pupa, including the gill. The envelope consists of thick, slimy threads that only become manifest after fixation in preservative (Wood 1978). This contrasts with the thin, discretely formed, darkened, threads of cocoons of most other simuliids. Second, the larval exuviae remains trapped between the gills by the surrounding gelatinous matrix. Both of these features seem to be unique, and are evidence of the monophyly of *Twinnia* (1). However, evidence presented later will show that *Twinnia* belongs to a monophyletic group including *Levitinia* and *Gymnopais*. The pupal cocoon of these latter 2 genera is in the form of a small ventral pad, to which the naked pupa remains attached to the substrate. I will suggest under the discussion of character 17 that a reduced cocoon is in the groundplan of *Levitinia* + *Twinnia* + *Gymnopais*, and that the conditon in *Twinnia* is a further modification of this general plan. Wood (*loc. cit.*) has indicated that the pharate pupa of *Gymnopais* is enveloped in the same slimy matrix as pharate pupal *Twinnia*, except that all but the ventral-most portion of this matrix disappears at pupation. If this is taken as the groundplan condition of *Levitinia* + *Twinnia* + *Gymnopais* , then the condition in *Twinnia* can be interpreted as a neotenic retention of the transparent envelope throughout the pupal stage[8]. A gelatinous cocoon might serve to protect a pupa should the spring in which it lives runs dry before development is completed (Wood 1978). Character states are coded as follows: **(0)** a well-developed cocoon consisting of darkened threads; **(1)** an ill-formed cocoon that is in the form of a small ventral pad; **(2)** a [illegible] that is in the form of a gelatinous envelope enclosing all of pupa, retaining larval exuviae.

3.6.8 Genus ***GYMNOPAIS*** Stone, 1949

GYMNOPAIS Stone, 1949: 260. Type species: *Gymnopais dichopticus* Stone, 1949, by original designation.

The genus *Gymnopais* was described for two remarkable new species discovered in Alaska (Stone 1949). Larvae of this segregate appeared different from all others known at the time by the complete absence of the labral fans, the primary feeding appendages of larval Simuliidae. Other life stages of *Gymnopais* were thought to agree with *Prosimulium s.lat.* in most respects, except as follows: absence of fine recumbent hairs on body, elongate petiole of M_{1+2}, a bulla near the posterior margin of the compound eye, and virtual absence of recurved hooks from the dorsum of the pupal abdomen.

Rubtsov (1955) was so impressed with the fanless condition of larval *Gymnopais*, he recognized a separate subfamily for members of that segregate, the Gymnopaidinae.

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[8] Beaucournu-Saguez and Braverman (1987) report that *Levitinia* and *Gymnopais* have the same type of pupal cocoon.

This action was presumably based on the assumption that black flies are derived from a chironomid ancestor (whose larvae also lack labral fans), and that the fanless condition in Simuliidae must therefore be primitive. However, as already indicated under the section on *Twinnia*, it is reasonably well established that the fanless condition in Simuliidae is actually derivative, and that *Gymnopais* and its fanless relatives are all derived from a *Prosimulium s.lat.* ancestor (Wood 1978).

Gymnopais species are extensively modified for life in high arctic or high alpine environments (Downes 1964, 1965). Females are all autogenous (their eggs being developed from nutrients stored during the larval stage); number of eggs produced is reduced (20-150, as compared to 200-500 in most other Simuliidae); mating takes place on the ground (as opposed to aerial mating as in most other Simuliidae); the male eye of most species is dichoptic, rather than holoptic (probably being correlated with mating on the ground); at least two species are parthenogenetic (freeing them from the necessity to mate in inhospitable environments); and adults are typically incapable of flight, or are at most very weak fliers (*G. holopticus* is the only species I am aware of that is capable of flight).

Many of the features used to characterize *Gymnopais* are no more than specializations to life in wind-blown localities. Various combinations of these same specializations are found in other groups of Diptera. For example, a reduced antenna and maxillary palpus, a flattened thorax, and enlarged terminalia (three characteristics of *Gymnopais*) have developed in parallel in three independently derived species groups of the chironomid genus *Diamesa* Meigen (Sæther 1986). Rubtsov (1974) used one of these characteristics (a flattened thorax) to help justify his supposition that *Gymnopais* is a link between Chironomidae and Simuliidae. However, caution should be used when evaluating characters that are subject to parallel selection.

Gymnopais immatures live in the headwaters of streams that either take their origin from permafrost areas, or from the bases of glaciers (Wood 1978, personal observation). Such water courses are characteristically very cold, not exceeding 5° C. In the absence of labral fans, larvae must graze their algal food from the stony substrates on which they live. Last-instar larvae do not spin a cocoon as such, and instead produce a small ventral pad to which the naked pupae remains attached to the substrate. Emergence is typically asynchronous, occuring over several weeks or even a month or more, depending on whether or not the species is parthenogenetic (the emergence period for sexual species is generally more truncated). Adults live from 3 to 5 days in the laboratory. It is unlikely that they take any form of nourishment in nature, other than water (Currie 1986). There is only one generation per year, with overwintering in the egg stage.

The 12 described species of *Gymnopais* are widely distributed in mountainous and high latitude areas of the Holarctic region. Palaearctic members range from central and southeastern Altai (*G. rubtzovi* Bobrova), east to Primorye (*G. sexcornutus* Bodrova), and north to Kamtchatka (*G. frontatus* Yankovsky). Apart from a single record of *G. bifistulatus* from northern Mongolia (Halgos 1978), all Palaearctic records of *Gymnopais* are from the USSR. All five Nearctic species are known from central Alaska and the Yukon (Beringia). One of these species, *G. holopticoides* Wood, is distributed from Beringia east to Labrador; another species, *G. dichopticoides*, is distributed from Beringia, south along the Rocky mountains to southeastern Alberta.

Monophyly of the genus *Gymnopais* Stone

Character 66.

General vestiture of adult sparse, short, erect. — The general vestiture of adults of *Gymnopais* consists of a sparse covering of short, coarse, erect (or semierect) setae (fig. 23, 24). Absent is the dense covering of fine recumbent setae (pile), characteristic of adults of all other Simuliidae. The apotypic state is clearly unique to *Gymnopais*, and is strong evidence of the monophyly of the genus (**1**). The primitive state is vestiture mainly of pile, with only a few, coarse, erect setae interspersed (**0**).

Character 67.

Clypeus nearly devoid of setae. — The clypeus of *Gymnopais* adults is devoid of setae centrally, and has only a few irregularly situated setae laterally (**1**) (fig. 23). Adults of all other Prosimuliini, like those of other simuliids, have the clypeus entirely covered with setae. Out-group comparison with other Chironomoidea indicates that this latter condition is primitive (**0**).

Character 68.

Mandible and lacinia of female without apical teeth. — As discussed under characters 9 and 32 of the second chapter, simuliid females are presumed to be primitively anautogenous (**0**). The mandible and maxillary lacinia of such females are variously serrated apically, adapting them for piercing the skin. Females of *Gymnopais* lack serrated mandibles and laciniae, which must be considered a secondary development (**1**). The apotypic state is a regressive feature that is subject to homoplasy, and is therefore not concincing as a phylogenetic indicator.

Character 69.

Thorax of adult slightly arched. — One of the most characteristic features of Simuliidae is the humped-backed appearance of adults. Adults are typically very strong fliers, and the markedly arched (and usually high) thorax contains well developed flight muscles (**0**). Field observations of Nearctic *Gymnopais* reveals that adults are either poor fliers (*G. holopticus*), or are incapable of flight altogether (*G. holopticoides, G. dichopticus, G. dichopticoides, G. fimbriatus*). The weakly arched thorax of *Gymnopais* species is probably related to the degenerate condition of the flight muscles, which must be considered derivative (**1**) (fig. 24). Certain specimens of *G. fimbriatus* were found to have virtually no flight muscles at all, and the female of that species was found to have eggs protruding into the thorax (personal observation).

Character 70.

Postnotum relatively small and markedly arched, with a variously distinct median longitudinal ridge. — The apotypic state is present only in members of *Gymnopais* (**1**) (fig. 15). The condition in other prosimuliines is for the postnotum to be larger and rather evenly arched dorsally, with no suggestion of a dorsomedian longitudinal ridge. Out-group comparison with other Simuliidae indicates that these latter two conditions are plesiotypic (**0**).

Character 71.

Anepisternal membrane with a small group of hairs. — The anepisternal (pleural) membrane is bare in *Parasimulium* and most members of the tribes Prosimuliini and Simuliini (**0**). *Gymnopais* adults are distinguished from those of most other simuliids by presence of a few setae on the anepisternal membrane (**1**) (fig. 24). Adults of *G. fimbriatus* apparently lack such setae (Wood 1978); however, other characters suggest that this could be a reversal toward the primitive conditon. The apotypic conditon has apparently been evolved independently in members of the simuliine genus *Metacnephia* Crosskey.

Character 72.

Mesepimeron with vestiture confined to dorsal part of sclerite above level of metathoracic spiracle. — *Gymnopais* adults have the vestiture of the mesepimeron (= mesepimeral tuft) confined to the dorsal-most portion of the sclerite, above the level of the ventral margin of the metathoracic spiracle (Wood 1978) (**1**) (fig. 24). This differs from the condition in other adult prosimuliines, in which the mesepimeral tuft is more extensive ventrally, extending into the area below the level of the metathoracic spiracle. I have interpreted this as the groundplan condition for Prosimuliini (**0**).

Character 73.

Wing membrane fumose and slightly wrinkled. — The wing of *Gymnopais* members is somewhat wrinkled, and has a pale smokey-brown appearance (nearly opaque in some specimens) (**1**). The opaqueness is evidently the result of microtrichia, which are particularly small and numerous on the wing membrane of *Gymnopais* (Wood 1978). In all other prosimuliines the wing is less wrinkled, and the membrane is hyaline. Out-group comparison with other Simuliidae indicates that these latter two conditions are primitive (**0**).

Character 74.

Petiole of M_{1+2} elongate, about half as long as petiole of Rs. — The petiole or stalk of veins M_{1+2} is exceptionally long in *Gymnopais*. It is about as half as long as the petiole of the radial sector (R_{2+3} and R_{4+5}), as compared to about one-fifth that length in other Prosimuliini. A short petiole is probably in the groundplan of Prosimuliini, as inferred from the occurrence of this conditon in Parasimuliinae and Simuliini (**0**). The elongate petiole in *Gymnopais* must therefore be derived, and can be taken as evidence of the common ancestory of its members. The apotypic state is shown on the prosimuliine wing illustrated in figure 20 of chapter 2.

Character 75.

Terminal plate of genital fork (= sternum 9) not connected directly to tergum 9. — The terminal plate of the genital fork of *Gymnopais* females is not directly connected with tergum 9. Instead, the tergum and sternum of that segment are distinctly separated by membrane (fig. 15). The only other simuliid that I am aware of with a similar condition is *Levitinia.* A membranous connection between the tergum and sternum of segment 9 is clearly derived with respect to other simuliids, which typically have a distinct sclerotized connection between these two sclerites (figs. 10-14). Although it might be argued that the apotypic state is evidence of the immediate common ancestory of *Levitinia* and *Gymnopais*, evidence presented later suggests that *Levitinia* is actually the sister group of *Twinnia* + *Gymnopais.* There are two possible interpretations: either the lack of a connection is a groundplan feature of the fanless prosimuliines, with subsequent reversal to the primitive form in *Twinnia*; or there have been two independent derivations of the apotypic state — once in *Gymnopais*, and once in *Levitinia.* The latter hypothesis is favored in this instance because loss of a connection is an easier step developmentally. The apotypic state is (1), the plesiotypic state is presence of a sclerotized connection (0).

Character 76.

Spermatheca basally with a short or long neck, to which the spermathecal duct is connected. — In the Prosimuliini groundplan the apex of the spermathecal duct is inferred to be connected with a variously sized membranous ring at the base of the spermatheca (0) (figs. 10-14). This is the condition in *Prosimulium, Helodon s.lat., Urosimulium, Levitinia,* and *Twinnia.* The spermatheca of *Gymnopais* females differs from the general plan in that the base is produced into a variously sized, sclerotized neck (fig. 15). This condition is clearly unique among prosimuliines, and is taken as evidence of the monophyly of *Gymnopais* (1).

Character 77.

Anal lobe and cercus of female fused into a single, solid sclerite. — *Gymnopais* females are unique among Prosimuliini in having the anal lobe and cercus fused into a single, solid sclerite (**1**) (fig 15). The typical condition is for the anal lobe and cercus to be clearly separated by membrane (figs. 10-14). Out-group comparison with Parasimuliinae and Simuliini indicates that this latter condition is primitive (**0**).

Character 78.

Gonostylus slender apically,with apical peg-like setae minute. — The gonostylus of males of *Gymnopais* is relatively narrow compared with that of other prosimuliines, and is tapered apically to an acute point. Further, the apical peg-like setae are so small that they are barely visible under magnification with a dissecting microscope (**1**) (fig. 22). The primitive condition for Prosimuliini is for the gonostylus to be relatively broad throughout, with a narrowly- to broadly- rounded apex, and for the apical peg-like setae to be readily visible under magnification with a dissecting microscope (**0**) (figs. 16-18, 21). The only other prosimuliine with a narrow gonostylus is the male of *Helodon* (*Distosimulium*); however, the apical peg-like setae are conspicuous in that subgenus (figs. 19, 20). Other characters, such as the unique clasping mechanism of the gonostylus of *Distosimulium*, suggests that any similarity with the gonostylus of *Gymnopais* is strictly due to convergence (see discussion of characters 58 and 59).

Character 79.

Sterna 4-7 of pupal abdomen each with up to 5 pairs of recurved hooks. — *Gymnopais* pupae have a relatively large number of sternal hooks compared to those of other prosimuliines. The exact arrangement of hooks varies among species, and even among individuals of the same species. However, the overall number of sternal hooks per *Gymnopais* pupa far exceeds the number in most other simuliid pupae (**1**) (fig. 8c). The typical prosimuliine pupa has no more that two pairs of hooks per sternum (**0**) (figs. 8a, 8b). The large number of hooks probably allows the *Gymnopais* pupa to remain attached to the small ventral pad of silk, which is all that remains of the pupal cocoon.

Character 80.

Pleurite 4 of pupal abdomen hardly differentiated from (or fused to) adjacent tergum and sternum. — *Gymnopais* pupae are unique in having abdominal pleurite 4 slightly differentiated from, or fused to, the adjacent tergum and sternum. In this respect segment 4 is similar in appearance to segment 3, which also has the pleurite fused to the tergum and sternum (see also discussion of character 46). As discussed under character 52 of chapter 2, presence of a discrete pleurite on each of abdominal segments 4 and 5 is interpreted as a groundplan feature of Prosimuliini. Hence, any connection between the pleurite with the adjacent tergum and sternum must be considered a secondary development (**1**). All other prosimuliine pupae have a narrow, but distinct, band of striate pleural membrane between the pleurite and the adjacent tergum and the sternum (**0**). A diagrammatic representation of some evolutionary transformations of the prosimuliine pupal pleuron is given in figure 6. Features of the pupal pleuron are considered in greater detail under the discussion of character 39.

Character 81.

Form of labrum and labropalatum of larva. — *Gymnopais* larvae are distinguished from those of other fanless prosimuliines by several features of the labrum and labropalatum. For the purposes of the present character analysis I have combined these features under a single character state. Synapotypic features of the *Gymnopais* labrum and labropalatum are considered individually below:

a) *Labrum conspicuously longer than wide.* — The *Gymnopais* labrum is proportionally longer and narrower than those of *Levitinia* and *Twinnia* (compare figs. 30 and 31). Because the condition in fanned prosimuliines is for the labrum to be short and broadly rounded apically (figs 32-34), I have interpreted the exceptionally long and narrow labrum of *Gymnopais* larvae as derivative (**1**).

b) *Labrum with a lateral transparent tubercle on each side.* — Another distinctive (and apparently autapotypic) feature of *Gymnopais* larvae is the conspicuous tubercle situated laterally on each side of the labrum (**1**) (fig. 31). No such tubercle is present on the labra of any other simuliid (**0**).(figs. 30, 32-34).

c) *Epipharyngeal apparatus with V-shaped brush anteriorly.* — *Gymnopais* larvae evidently have a unique arrangement of hairs on the ventral surface of the epipharyngeal apparatus. The anterior-most setae are organized into a distinct V-shaped structure, which is readily visible in ventral view (Wood 1978) (**1**). The anterior-most setae of the labra of *Levitinia* and *Twinnia* are more irregularly situated, and are not organized into a V-shaped structure. I have interpreted this latter condition as plesiotypic (**0**).

3.7 Relationships among genus-group taxa of Prosimuliini

3.7.1 Monophyly of Prosimuliini, exclusive of *Prosimulium* *s.str.*

Character 10.

Claw of female with a distinct, basal or subbasal tooth. — The taxonomic value of the female tarsal claw has long been recognized (Rubtsov 1940, 1964, 1974). The claw is of greatly varied length and shape, and may be either simple (fig. 26), or possess a variously sized basal or subasal tooth (fig. 27). Differences in the claw have been used to distinguish not only species, and groups of species, but higher taxa as well. Indeed, Rubtsov (1940) lists the tarsal claw as the single most important diagnostic feature of Simuliidae! While the relative merits of this character system is open to debate, there can little doubt about its importance as a phylogenetic indicator. However, there is an extreme amount of homoplasy within the family, and so hypotheses about relationship must be based on careful reference to the defined out-groups.

Rubtsov (1940), in addressing the character polarity of the female tarsal claw, concluded that claws with a conspicuous basal tooth (*e.g. Simulium vernum* Maquart), and those that are simple (*e.g. S. reptans* (Latreille) and *S. equinum* (Latreille)), are both plesiotypic. The presumed derived condition are claws that have a small basal or subbasal tooth. In support of this hypothesis, Rubtsov indicates that the 2 'primitive' types of claw are clearly formed early in pupal development — an example of 'ontogeny recapitulating phylogeny'. In his 1974 paper, Rubtsov realized that the distribution of character states was much more complex than originally supposed, and that a conspicuous basal tooth was best regarded as a secondary development in certain taxa.

It is difficult to imagine how two completely different character states (*i.e.* a simple versus a complex tarsal claw) can simultaneously be construed as primitive. Out-group comparison with other Chironomoidea reveals that a simple type of claw is the only one in females of Thaumaleidae and Chironomidae. In Ceratopogonidae the pattern is rather more complex, with the female tarsal claw either simple, or with a variously sized basal or subbasal tooth. However, a simple claw is evident in the 2 most primitive clades of Ceratopogonidae (*viz.* Leptoconopinae[9] and Austroconopinae), and so a simple female claw is probably basic to that family as well. Within Simuliidae, a simple claw (or one with a minute basal or subbasal tooth) is characteristic of *Parasimulium*, *Prosimulium s.str.*, and many simuliines, and so I can conclude only that a simple claw represents the primitive condition. A complex tarsal claw must therefore be derivative, and is used to define monophyletic lineages within Simuliidae.

The evolutionary significance of a basal or subbasal tooth was speculated upon by Shewell (1955). He concluded that the vast majority of species with simple or minutely toothed claws attack mammals, whereas those with distinctly toothed claws feed principally upon the blood of birds. It was suggested that the tooth adapts the claw for movement beneath feathers, and that it might also prevent the claw from becoming entangled in the plumage. Unfortunately, there have been relatively few studies about blood-feeding behaviour of female prosimuliines, although most reports seem to support the general pattern described by Shewell. Females of *Helodon*, *Parahelodon*, and *Distosimulium* (all of which have a large basal tooth in their groundplan) have all been reported as blood-feeders upon birds (Bennett 1960, Peterson 1970, Sasaki *et al.* 1986). The feeding habits of females of *Urosimulium*, which also have a large basal tooth, are evidently not known. The female of *Levitinia* has a small, but distinct, tooth on the tarsal claw, but nothing is known about its hosts. *Twinnia* females have simple tarsal claws, and have been reported as blood-feeders upon humans, horses, and deer (Dyar and Shannon 1927, Currie 1986, Sasaki *et al.* 1986). All species of *Gymnopais* have a simple female claw, and are reported to be autogenous.

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[9] The female claw of *Leptoconops* (*Leptoconops* Skuse) bears a basal tooth or bristle, but this is probably non-homologous with similar structures in other Ceratopogonidae.

To summarize, a simple tarsal claw is characteristic of *Prosimulium s.str.*, *Twinnia* and *Gymnopais*, whereas a variously sized (but conspicuous) tooth is typically present on the female claw of all other genus-groups. Evidence presented later in this chapter will suggest that *Levitinia*, *Twinnia*, and *Gymnopais* form a monophyletic group, with *Levitinia* forming the sister taxon of *Twinnia* and *Gymnopais* together. Because the female of *Levitinia* has a distinct basal tooth on the claw, I have concluded that its absence from *Twinnia* and *Gymnopais* must be the result of reduction or loss. On the other hand, there are no intermediates to suggest that the simple claw of female *Prosimulium s.str.* is also the result of loss (*i.e.* there is no evidence to suggest that that a toothed claw is actually in the groundplan of Prosimuliini as a whole). I have therefore concluded that a simple claw is primitive for Prosimuliini, and that a claw with a conspicuous basal tooth is evidence of the monophyly of Prosimuliini, exclusive of *Prosimulium*.

Although a large basal tooth can be assigned reasonably to the groundplan of *Helodon s.lat.*, the tooth has evidently become secondarily lost in some species. For example, on overall balance of characters, it would seem best to assign *Prosimulium aridum* Rubtsov to *Helodon s.lat.*; however, the female of that species has only a minutely toothed claw[10]. A possible explanation for this incongruity comes from examination of the female mouthparts. The mandible and maxillary lacinia of *P. aridum* are completely devoid of retrorse hooks apically, and are thus rendered incapable of piercing the skin. As discussed under character 32 in chapter 2, blood feeding is presumed to be a primitive feature of Simuliidae, and so autogeny must be considered a secondary or derivative feature. Having lost the ability to blood feed, the female of *P. aridum* no longer has the need for a largely toothed claw, and so the tooth has presumably become reduced over time. The same argument can also be applied to the autogenous female of *Prosimulium phytophagum* Rubtsov, which also lacks a conspicuous basal tooth on the tarsal claw. This species seems best assigned to *Helodon s.lat.* because it lacks any of the autapotypies attributable to other Prosimuliini genus groups.

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[10] *Prosimulium aridum* Rubtsov is only known in the female stage.

In summary, the initial dichotomy is apparently between prosimuliines whose females are mammalophilic (*Prosimulium*), and those whose females are primitively ornithophilic (Prosimuliini, exclusive of *Prosimulium*). Several members of this latter group have evidently reverted back to mammalophily, or have lost the ability to blood-feed altogether. In such instances the basal or subbasal tooth of the female tarsal claw has become reduced, or even lost. The apoptypic state has evidently been derived several times indedendently in various lineages of Simuliini. Character states are coded as follows: (**0**) female claw simple; (**1**) female claw with a distinct basal or subbasal tooth; (**2**) female claw with basal tooth lost.

3.7.2 Monophyly of *Helodon s.lat.* (*Helodon s.str. Parahelodon, Distosimulium*)

Character 11.

Chromosomes with fixed inversions IIIL-1 and 1 x IIS. — Although the overall close relationship between *Helodon*, *Parahelodon*, and *Distosimulium* has not been questioned, I have not been able to find convincing (synapotypic) structural characters to unite them. The monophyly of the group is therefore supported solely on cytological grounds. In his chromosome transformation series of "Prosimuliinae", Rothfels (1979) characterized *Helodon s.lat.* members as having the fixed inversions IIIL-1 and 1 x IIS. These inversions are evidently unique, and are taken as evidence of the common ancestory of *Helodon s. lat.* Two cytological subgroups were recognized within this group: one, including the nominate subgenera *Parahelodon* and *Distosimulium*; and another including members of *Helodon s. str.* (fig. 2). Presence of fixed inversions IIIL-1 and 1 x IIS is coded (**1**); absence of those inversions is coded (**0**).

3.7.3 Monophyly of *Urosimulium* + the fanless Prosimuliini (*Levitinia, Twinnia, Gymnopais*).

Character 12

Mandible of larva with apical brush of bristle-like setae. — The apical mandibular brush is a series of hairs situated immediately basad of the apical teeth on the ventral surface of the mandible. Currie and Craig (1987) have suggested that, during browsing, the apical brush is drawn past the leading (toothed) edge of the hypostoma in a "pan and broom" fashion. Algae and other types of deposited organic matter are thereby swept off the substrate, and into the cibarium. Primitively, the apical brush consists of a series of rows of fine hair-like setae, such as in larvae of *Parasimulium*, *Prosimulium s. str.* and *Helodon s.lat.* (*cf.* fig. 27 of chapter 2). The condition in *Urosimulium* larvae differs from the one described above in that the apical brush is comprised of shorter, thicker, bristle-like setae. In this respect the apical brush of *Urosimulium* seems to represent an intermediate stage of a transformation series between the presumed primitive configuration, as characteristic of the majority of simuliids examined, and the stout, spine-like, setae that comprise the apical brush of *Levitinia* and *Gymnopais* larvae (fig.36). The more extensive apical brush of fanless Prosimuliini is undoubtedly related to the obligate scraping habit of the larvae. The apical mandibular brush of *Twinnia* larvae consists of 2 types of setae; an anterior row of 3 or 4 spine-like setae, and several more posterior rows of bristle-like setae. I have suggested under the discussion of character 64 that the condition in *Twinnia* may be a reversal from the type of mandible of *Levitinia* and *Gymnopais*. Character states are coded as follows: (0) apical brush consisting of lone, fine setae; (1) apical brush consisting of bristle-like setae; (2) apical brush consisting of spine-like setae; (3) apical brush with spine-like setae reduced.

Character 13.

Anal sclerite with a short, posteromedially directed projection between posteroventral arms. — The anal sclerite has been interpreted as a groundplan apotypy of Simuliidae (see discussion of character 20 in chapter 2). Primitively the anal sclerite is an X-shaped structure that consists of a median sclerite and 4 radiating arms — 2 anterodorsal and 2 posteroventral. This pattern appears to be basic to all major lineages of Simuliidae, including Prosimuliini. An X-shaped anal sclerite characterizes all members of *Prosimulium s.str.*, all members of *Helodon s.str.*, both species of *Helodon* (*Distosimulium*) and one species of *Helodon* (*Parahelodon*) (subrectangular shaped in the other 2 species) (fig. 9a). The anal sclerite of *Urosimulium* larvae differs from the basic plan in that it has a small, posteromedial projection arising from the median sclerite between the posteroventral arms (fig. 9b). Other character states of prosimuliines include an inverted star-shaped anal sclerite (*Levitinia*; fig 9c) and a Y-shaped anal sclerite (*Twinnia* and *Gymnopais*; fig. 9d). Developmentally, the type of anal sclerite in *Urosimulium* larvae is the most easily derivable from the plesiotypic form: all that would be required is development of a short, posteriorly directed, sclerotized, projection between the posteroventral arms. If this can be accepted as a logical first step, then the inverted star-shaped sclerite of *Levitinia* could be derived easily through lengthening and widening of this posteromedially directed process (see also discussion of character 42). The Y-shaped anal sclerite of *Twinnia* and *Gymnopais* larvae could also be derived from the type of anal sclerite found in *Urosimulium*, through reduction or loss of the posteroventral arms, and development of an elongate, common base for the anterodorsal arms (see also discussion of characters 49 and 50). These are the interpretations followed in the present work. Character states are coded as follows: (**0**) anal sclerite X-shaped; (**1**) anal sclerite X-shaped with a short, supernumerary, posteromedially directed process; (**2**) anal sclerite with supernumerary process in the form of a prominent arm, subequal in length with anterodorsal and posteroventral arms; (**2´**) anal sclerite with posteroventral arms reduced, and with anterodorsal arms borne on an elongate common base (= median sclerite). The evolutionary transformations described above are illustrated in figure 9.

3.7.4 Monophyly of the fanless Prosimuliini (*Levitinia, Twinnia, Gymnopais*)

Character 17.

Cocoon rudimentary. — The cocoon is one of the most conspicuous features of black-fly pupae. In the simuliid groundplan, the cocoon is an irregular, thin- to thickly woven silken sac, enclosing all of the pupal abdomen and typically most of the thorax. This condition, which must be considered primitive, is characteristic of *Parasimulium, Prosimulium, Helodon s.lat.*, and most plesiotypic genera of Simuliini (**0**). The pupal cocoon of *Levitinia* and *Gymnopais* is rudimentary in comparison with those of most other simuliids because most of it sloughs at the time of pupation (Wood 1978). All that remains is a small ventral pad to which the naked pupa remains attached to the substrate (**1**). The only other simuliids with a similar arrangement are members of *Crozetia* and *Tlalocomyia;* however, other characters suggest that this must be an independent modification from the simuliid groundplan. The *Twinnia* pupal cocoon is in the form of thick, gelatinous, transparent strands, that cover the entire pupa in a slimy envelope (Wood 1978). As discussed under character 65, this is considered to be a further modification of the condition in *Levitinia* and *Gymnopais* (**2**).

Character 18.

Abdominal terga 4 and 5 of pupa each without an anterior row of posteriorly directed spines (= spine combs). — As discussed under character 48 of the second chapter, spine combs are interpreted as a groundplan feature of Simuliinae (*cf.* figs. 52 and 53 in chapter 2). Primitively, spine combs are situated on each of abdominal segments 4 to 9 (fig. 7a). This is the condition in *Prosimulium*, *Helodon s.str.*, *H.* (*Parahelodon*), *H.* (*Distosimulium*), *Urosimulium*, and many Simuliini. In the only pupa of *Levitinia* known, spine combs are lacking from each of abdominal terga 4 and 5, but are present on terga 6-9 (minute on terga 9 of specimen examined) (fig. 7b). Pupae of *Twinnia* and *Gymnopais* lack spine combs spine combs altogether (figs. 7c, 7d). I have interpreted the condition in *Levitinia* as forming part of a transformation series between the complete onchotaxy, typical of pupae of *Prosimulium*, *Helodon s.lat.* and *Urosimulium*, and the total absence of spine combs from pupae of *Twinnia* and *Gymnopais*. The primitive state is (**0**); loss of spine combs on pupal abdominal segments 4 and 5 is (**1**); and loss of spine combs altogether is (**2**) (see also discussion of character 48). Reduction in the number of spine-comb rows is probably correlated with the reduction of the pupal cocoon. The evolutionary transformations discussed above are summarized in figure 7.

Character 19.

Labral fans absent from second through final instars. — The form of the larval head is one of the most characteristic features of fanless prosimuliines. Not only are labral fans absent from most larval instars, but the shape of the head is modified for scraping, rather than filter feeding (compare figs. 30 and 31 with figs. 32-34). Although there would seem to be a substantial phylogenetic gap between fanless- and fully-fanned simuliids, Craig (1974) has shown that the two types of head are extremely similar in the first instar. For example, first instars of *Twinnia, Gymnopais, Prosimulium s.str., Helodon s.str.*, and *Crozetia* all have simple labral fans (*i.e.* the fan base is rudimentary or lacking, and only 0-4 fan rays are present), and the head appears rather ovoid in dorsal view. This same type of arrangement has subsequently been confirmed for first instars of *Parasimulium stonei* Peterson (Borkent and Wood 1986). The fan of other first instar simuliids, although somewhat more complex than in the taxa listed above, is still less complex than those of later instars. Wood (1978) has suggested that reduction of fans in the first instar may be a characteristic of the entire family, and I concur. The small size of the first-instar larva, and the thickness of the boundary layer around the larva's body, makes filter feeding in that stage unlikely (Currie and Craig 1987). For some as yet unknown reason, the fans are not fully expressed until the later instars.

Larvae of *Levitinia, Twinnia,* and *Gymnopais* are derived with respect to most other simuliids in that their fans are suppressed throughout the entire larval stage — not just in the first instar. This adapts larvae for life in the headwaters of streams, where settled food is more abundant than suspended food (Wood 1978, Currie and Craig 1987). Later instar larvae of *Crozetia crozetensis* Womersley, *Simulium oviceps* Edwards, and *S. neoviceps* Craig all have heads that are similarly structured, but at least a few labral-fan rays are present in each of these species. Other characters indicate no close relationship between any of these species and fanless prosimuliines. Suppression of the labral fans in all larval instars has undoubtly been derived several times independently in simuliids.

In addition to the complete absence of labral fans in second through final-instar larvae, there are a number of related modifications to the larval head of fanless Prosimuliini. These are considered individually below. Apotypic states are illustrated in figures 30 and 31; plesiotypic states are illustrated in figures 32-34:

a) *Head widest near base, ovoid in dorsal view.* — Head rather parallel-sided in other simuliids.

b) *Labrum elongate, terminating in a greatly pronounced palatal brush.* — Labrum shorter, with an inconspicuous palatal brush in other simuliids.

c) *Ecdysial line broadly V-shaped posteriorly.* — Ecdysial line broadly U-shaped posteriorly in most other simuliids; but broadly V-shaped in *Crozetia*, *Simulium oviceps*, and *S. neoviceps*.

All of these features are derived with respect to to other simuliids, and comprise evidence of the common ancestry of *Levitinia, Twinnia,* and *Gymnopais* (**1**). The plesiotypic state is denoted by (**0**).

Character 20.

Head of larva with posterior frontolabral muscles (61) each divided into two fascicles. — In Simuliidae, as in other Culicomorpha, the posterior frontolabral muscles (61) are inserted anteriorly on the messors, and originate posteriorly near the posterior margin of the frontoclypeal apotome. Contractions of these muscles control the movement of the labral fans. Anteriorly, the muscles are in the form of a single fascicle; posteriorly, they are divided into 2 or more fascicles. Craig (1974) recognized two basic arrangements in his study of the labrum of larval simuliids. In all fully-fanned simuliids examined, the posterior frontolabral muscles (61) is divided into 3 fascicles posteriorly. The fanless larvae of *Twinnia* and *Gymnopais* have only 2 fascicles posteriorly. This latter condition has now been confirmed for *Levitinia* as well. The frontolabral muscle (61) of Dixidae is similar to the type of fanned simuliids in that there are 3 fascicles posteriorly, and so I have interpreted this condition as primitive (**0**). Presence of only 2 fascicles must therefore be derived (a loss), and can be taken as a synapotypy of the fanless Prosimuliini (**1**).

Character 21.

Head of larva with ventral fascicles of posterior frontolabral muscles (61) not interdigitated. — As discussed under character 20 above, the posterior frontolabral muscles are each divided into 2 or more fascicles posteriorly. Craig (1974) has shown that, in fanned simuliids, the posterior fascicles of the right and left muscles are fully interdigitated. This contrasts with the condition in *Twinnia* and *Gymnopais*, in which the posterior fascicles do not interdigitate posteriorly. I have confirmed this latter condition for *Levitinia* as well. As discussed under character 16 in chapter 2, I have interpreted the interdigitated condition as a synapotypy of Simuliidae (**0**). The condition in *Levitinia, Twinnia,* and *Gymnopais* must therefore be considered a reversal toward the primitive conditon (**1**).

Character 22.

Mandible of larva broad apically, with flattened, evenly sized apical teeth. — The basic form of the larval mandible is very similar in *Levitinia, Twinnia,* and *Gymnopais*. It is relatively broad apically, and bears a number of flattened, more or less equally sized, blade-like teeth (**1**) (fig. 35-36). In most other simuliid larvae the mandible is rather more slender apically, and the teeth are more conical and pointed. Further, the teeth are of rather unequal length, with one tooth (the apical mandibular tooth) being the most prominent (cf. fig. 27 of chapter 2). Out-group comparison with other Culicomorpha reveals that the latter conditon is primitive (**0**). Currie and Craig (1987) discuss how the derived mandible adapts larvae for scraping algae and other organic matter from the substrate on which they live.

Character 23.

Mandible of larva with apical brush extensive, consisting of numerous rows of spine-like setae. — The larval mandible of simuliids has a series of rows of flattened setae or bristles on the aboral or ventral surface — the so-called apical mandibular brush (Craig

1977). Typically, the apical brush consists of slender setae that are arranged in several rows immediately basad of the apical mandibular teeth (*cf.* fig. 27 of chapter 2). The type of mandible found in *Levitinia* and *Gymnopais* differs from this basic plan in that the brush is much more extensive basally, consisting of 7-10 or more rows of setae. Another major difference is that the setae are in the form of stout, conical, spine-like outgrowths of cuticle (fig 36). Both of these features are clearly adaptations to scraping (Currie and Craig 1987), and must be considered derivative.

The apical mandibular brush of *Twinnia* larvae appears to be intermediate in form between the two types described above. It has a distal row of 3 or 4 spine-like setae (similar in form to the setae found in *Levitinia* and *Gymnopais*), and an additional 3 or 4 rows of slender, bristle-like setae (similar in form the setae found in *Urosimulium*; see character 12). It is suggested later in this chapter that *Levitinia* is the sister taxon of *Twinnia* + *Gymnopais*, and so it seems possible that the apparent intermediate condition in *Twinnia* is actually the a reversal from the form found in *Levitinia* and *Gymnopais* . This is the interpretation followed in the present work. Character states area coded as follows: (**0**) apical brush consisting of long, fine setae; (**1**) apical brush consisting of bristle-like setae; (**2**) apical brush consisting of spine-like setae; (**3**) apical brush with spine-like setae reduced.

Character 24.

Mandible of larva with covering-, first external-, and second external brushes reduced or lost. — The simuliid larval mandible typically possesses a series of 4 brushes that serve to comb the labral fan: the "covering brush", the "apical brush", the "first external brush", and the "second external brush" (Chance 1970) (cf. fig. 27 of chapter 2). In fanless Prosimuliini, the 4 brushes are either modified (see discussion of character 23 above) or reduced. For example, the larval mandible of *Twinnia* has apparently lost the covering- and second external- brushes, and has the first external brush of shorter, smaller bristles than found in filter-feeding larvae (Chance *loc. cit.*). The larval mandibles of *Levitinia* and *Gymnopais* are similarly modified. The reduced or modified condition of mandibular brushes is undoubtedly related to the loss of the labral fans (see discussion of character 19). Presence of 4 well-developed mandibular brushes is (**0**), presence of reduced or modified mandibular brushes is (**1**).

Character 25.

Hypostoma of larva with teeth dorsoventrally flattened, blade-like, and slightly sclerotized; not inclined dorsally. — The larval hypostomae of *Levitinia, Twinnia,* and *Gymnopais* are all similar in that they bear an apical series of flattened, blade-like, slightly sclerotized teeth (figs. 30, 31). Another distinctive feature is that the teeth are all perpendicular to the ventral wall of the hypostoma. This type of hypostoma serves as a "pan" into which algae and other organic matter is swept by the "broom-like" mandibles (Currie and Craig 1987). Although other larval simuliids are capable of feeding in a similar fashion, their teeth are rather more conical and pointed apically, and the median tooth is inclined dorsally (figs. 37, 38). As a consequence of this arrangement, the typical fanned larva is not able to browse as efficiently as fanless larvae. The "pan" type of hypostoma is clearly adapted for scraping, and can be considered a synapotypy of *Levitinia, Twinnia,* and *Gymnopais* (**1**). The only other prosimuliine with a similar of arrangement is the larva of *Helodon* (*Distosimulium*) *pleuralis* (fig. 39). However, the median hypostomal tooth of that species is inclined dorsally, and its nominal sister species, *H.* (*Distosimulium*) *daisetesensis,* has the typical hypostomal configuration for Prosimuliini. It therefore seems clear that the similarity is due to convergence, and is not evidence of a close relationship. The "pan" type of hypostoma has evidently been evolved several times independently in fanless members of Simuliini (*e.g. Crozetia* Davies, members of the *Simulium oviceps* Edwards group).

Character 26.

Hypostoma of larva with median tooth relatively short, its apex not extended anteriorly beyond apex of shortest lateral or sublateral tooth. — In larvae of fanless Prosimuliini, the median hypostomal tooth is relatively short compared to the lateral and sublateral teeth, giving the hypostoma a concave appearance medially (figs. 30, 31). In larvae of fanned Prosimuliini, the median tooth is typically longer than the one just described, with its apex extended anteriorly beyond the apex of the shortest lateral or sublateral tooth (fig. 37). Out-group comparison with *Parasimulium* and Simuliini indicates that this latter state is plesiotypic (**0**). The only other prosimuliines with a short median tooth are members of *Parahelodon* and *Distosimulium* (figs. 38, 39); however, other differences in the hypostoma suggests that this might be an indedendent modification from the general plan (see discussion of 25 above). Therefore, I have interpreted the apotypic state as being derived twice — once in *Distosimulium* + *Parahelodon,* and once in the fanless prosimuliines (**1**).

Character 27.

Postgenal cleft rudimentary or absent. — I have argued previously the postgenal cleft is a constitutive feature of members of Simuliinae (see discussion of character 50 in chapter 2). This feature of the larval head is present in most simuliines, and all fanned prosimuliines. Within this latter group, the cleft is either inverted U- or V-shaped, or is in the form of a shallow subrectangular notch (**0**) (figs. 32-34). In fanless members of Prosimuliini (*i.e. Levitinia, Twinnia, Gymnopais*) the postgenae are completely sclerotized medially and posteromedially, and the cuticle of the posteroventral margin of the headcapsule appears wrinkled. I have suggested that the cleft has become lost from members of the fanless Prosimuliini, and that the loss is correlated with loss of the labral fans (**1**) (see discussion of character 50 in chapter 2). The postgenal cleft has evidently become lost independently in members of the simuliine genus *Gigantodax* (in part).

Character 28.

Abdomen of larva with segments 1-4 narrow and ventrally "corrugated", expanded abruptly at segment 5, and tapered posteriorly to a small posterior proleg. — This type of abdomen, which provides the flexibility necessary for the body to bend in a tight U-shape, is an adaptation of scraping simuliids (Currie and Craig 1987) (**1**). It allows the browsing of a broad C-shaped (rather than a narrow U-shaped) area around the larva's point of attachment. The fanless larvae of *Levitinia, Twinnia* and *Gymnopais* all have this type of body form. The larval body of fanned prosimuliines is typically more evenly tapered posteriorly, and the abdomen is not "corrugated" ventrally (**0**). Further, the posterior proleg is proportionally larger than in members of the fanless Prosimuliini. Although most fanned larvae occasionally resort to browsing, they cannot forage as efficiently at any given point of attachment. Evidently, the derived body form has been evolved independently in fanless members of Simuliinii (*Crozetia* Davies, members of the *Simulium oviceps* Edwards group).

3.7.5 Monophyly of *Parahelodon* + *Distosimulium*

Character 31.

Arm of genital fork (= sternum 9) slender, with a pronounced terminal plate. — The genital fork of females of *Parahelodon* and *Distosimulium* is distinguished by slender arms, and by the markedly pronounced terminal plate that arises from the apex of each arm (figs. 12, 13). Indeed, the terminal plate of *Distosimulium* females is so large that it projects conspicuously beyond the posterior margin of the hypogynial valves. In other Prosimuliini females, the arm of the genital fork is typically rather broad, and the terminal plate is comparatively small (*i.e.* never projecting posteriorly beyond the posterior margin of the hypogynial valves) (figs. 10, 11, 14, 15). Out-group comparison with *Parasimulium* and simuliine females indicates that this latter condition is primitive (**0**). The combination of a slender arm and a greatly pronounced terminal plate must therefore be derived (**1**), and is taken as evidence of the common ancestory of *Parahelodon* and *Distosimulium*.

Character 32.

Median sclerite of aedeagus with arms fused together apically. — The median sclerite is a strap-like extension of the dorsal surface of the ventral plate (figs. 16-18, 20-22). It is articulated mediobasally with the plate, and projects posterodorsally as a midventral support for a cone-like structure that bears at its apex the extensible gonopore (Wood and Borkent 1982). Primitively, the median sclerite is a Y-shaped structure that has its simple end articulated with the ventral plate (**0**) (figs. 16, 17, 21, 22). In Parasimuliinae the sclerite is only shallowly notched apically, and this may possibly represent the groundplan condition for Simuliidae. In Simuliinae, the arms are typically distinctly separated. The median sclerite of *Distosimulium* and *Parahelodon* differ from those of most other simuliids in that the arms fused together apically (figs. 18, 20). However, there still remains a variably distinct space or groove between the two arms. This condition is clearly unique among prosimuliines, and is taken as evidence of the common ancestry of *Distosimulium* and *Parahelodon* (**1**).

Character 33.

Paramere not connected to anterolateral apodeme of ventral plate. — In the simuliid groundplan the paramere is connected to both the anterolateral apodeme of the ventral plate, and the anterodorsal margin of the gonocoxite (the gonocoxal apodeme). As discussed under character 60 of chapter 2, the paramere is typically connected to the anterolateral apodeme by a variously sized, sclerotized strap. A long, distinct "strap-like connection" is characteristic of most male prosimuliines except *Distosimulium* , *Parahelodon*, and *Levitinia* (0) (figs. 16, 17, 21, 22). The paramere in these latter three groups lacks any suggestion of a strap-like connection with the anterolateral apodeme, and they are instead simply fused to the gonocoxal apodeme (1) (figs. 18, 20). Other characters suggest that the apotypic condition has been derived twice in Prosimuliini: once in *Levitinia* (character 38), and once in *Parahelodon* + *Distosimulium*. The parameral connection has also been lost independently from certain members of Simuliini.

Character 34.

Hypostoma with median tooth relatively short, its apex not extended anteriorly beyond apex of shortest lateral or sublateral tooth. — The form of the larval hypostoma of *Distosimulium* and *Parahelodon* is distinctive among the fanned Prosimuliini. The median tooth is relatively short compared to the lateral and sublateral teeth, giving the hypostoma a concave appearance medially (figs.38, 39). In other fanned prosimuliines the median tooth is typically longer than the one just described, with its apex extended anteriorly beyond the apex of the shortest lateral or sublateral tooth. Indeed, the median hypostomal tooth of *Helodon s.str.* is typically the longest (fig.37). In comparison with other fanned prosimuliines, therefore, a short median hypostomal tooth is clearly derived (1). A short median hypostomal tooth is also evident in the fanless prosimuliines (figs. 30, 31), and so it is possible that the apotypic state is indicative of a more inclusive monophyletic group. However, there are other differences in the hypostoma that might suggest indedendent development of the derived condition (see discussion of character 25). For reasons described more fully below, I have interpreted the apotypic state as being derived twice — once in *Distosimulium* + *Parahelodon,* and once in the fanless prosimuliines.

3.7.6 Monophyly of *Gymnopais* + *Twinnia*

Character 43.

Flagellum of antenna of 7 articles. — Adults of *Twinnia* and *Gymnopais* are distinguished from most other Prosimuliini by their 7-articled flagellum (fig. 23). A 9-articled flagellum is the most common condition in Prosimuliini, although 8-articles characterize isolated species [*Helodon (Parahelodon) decemarticulatus* (Twinn), *Prosimulium unicum* Twinn]. A 9-articled flagellum has been interpreted as the groundplan condition for Simuliidae, and so the lesser number must be considered derivative in *Twinnia* and *Gymnopais* (see discussion of character 2 in chapter 2). The only other prosimuliine with a 7-articled flagellum is *Helodon (Parahelodon) gibsoni;* however, other characters indicate that there is no close relationship between this species and *Twinnia* and *Gymnopais*. Character states are coded as follows: (**0**) a 9-articled flagellum; (**1**) an 8-articled flagellum; (**2**) a 7-articled flagellum.

Character 44.

Stemmatic bulla near posterior margin of compound eye. — As already discussed under character 24 of chapter 2, the stemmatic bulla is a remnant of the larval eye (fig. 23). A prominent bulla apparently has been developed twice in Simuliidae — once in *Parasimulium*, and once in *Twinnia* and *Gymnopais* (**1**). The primitive condition in Simuliidae is for the the stemmatic bulla to be absent (**0**).

Character 45.

Tarsal claw of female without basal or subbasal tooth. — A tarsal claw with a distinct basal or subbasal tooth is presumed to be the groundplan condition for Prosimuliini, exclusive of *Prosimulium s.str.* (see discussion of character 10) (fig. 27). Such a condition characterizes the female of *Levitinia*, which has a tooth about 1/4 the total length of the claw. If *Twinnia* and *Gymnopais* share an immediate common ancestor with *Levitinia* (and all available information points to this conclusion), then absence of a subbasal tooth must be interpreted as a loss (fig. 26). Character states are coded as follows: (**0**) female claw simple; (**1**) female claw with a distinct basal or subbasal tooth; (**2**) female claw with basal tooth lost.

Character 46.

Segment 3 of pupal abdomen ring-like, the terga and sterna of that segment fused together laterally. — Pupae of *Twinnia* and *Gymnopais* are unique among Prosimuliini in having the tergite and sternite of abdominal segment 3 fused together laterally (**1**) (figs. 6c, 6d). In all other prosimuliine pupae, abdominal segment 3 is divided laterally by pleural membrane. This latter condition has been interpreted as part of the prosimuliine groundplan, and must be considered primitive (**0**). Features of the prosimuliine pupal pleuron have been considered in greater detail under the discussion of character 39. The evolutionary transformations discussed above are illustrated in figure 6.

Character 47.

Terga 3 and 4 of pupal abdomen with recurved hooks reduced or lost, occupying a position between the middle of the tergum and its posterior margin. — A characteristic feature of simuliid pupae is the presence of 4 pairs of anteriorly directed hooks along the posterior margin of each of abdominal tergites 3 and 4. This pattern is probably basic to Prosimuliini, as suggested by its presence in the following lineages: *Prosimulium, Helodon s.lat., Urosimulium* and *Levitinia* (**0**) (figs. 7a, 7b). *Twinnia* and *Gymnopais* pupae can be distinguished from those of other Prosimuliini by presence of a maximum of 3 pairs of hooks per tergite; and instead of the hooks occupying the posterior-most margin of the tergite, as in most other Simuliidae, they are situated between the middle and posterior edge of the tergite (figs. 7c, 7d). This arrangement is clearly unique, and is evidence of the monophyly of *Twinnia + Gymnopais*. The tergal hooks of *Gymnopais* pupae are less well developed than they are in *Twinnia* pupae, and Wood (1978) has suggested that they may have become vestigial because there is no longer a cocoon for the hooks to be attached to.

Character 48.

Terga 5-9 of pupal abdomen each without an anterior row of posteriorly directed spines (= spine combs). — This is the third stage of a transformation series that begins with the complete pupal onchotaxy of *Prosimulium s.str.* and *Helodon s.lat.* (spine combs on each of abdominal terga 4 - 9) (**0**) (fig. 7a). An intermediate condition characterizes the pupa of *Levitinia,* which only has spine combs on terga 6 - 9 (**1**) (fig. 7b). If this latter state is interpreted as the groundplan condition for the fanless prosimuliines, then complete absence of spine combs from *Twinnia* and *Gymnopais* must be considered a further derived state (**2**) (figs. 7c, 7d). The transformations discussed above are considered in greater detail under character 18.

Character 49.

Anal sclerite with posteroventral arms rudimentary or absent. — The Y-shaped anal sclerites of *Twinnia* and *Gymnopais* larvae are distinguished by the rudimentary appearance of the posteroventral arms. They are either lacking entirely, or are represented by a short protuberance on either side of the "stem" near the base (fig. 9d). As discussed under character 13, the posteroventral arms are presumed to be well developed in the Prosimuliini groundplan (**0**) (figs. 9a-9b). The rudimentary form of the posteroventral arms must therefore be the result of reduction or loss, and thus is evidence of the common ancestry of *Twinnia* and *Gymnopais* (**1**). Larvae of *Helodon* (*Parahelodon*) *decemarticulatus* and *H.* (*P.*) *gibsoni* evidently have lost both the anterodorsal and posteroventral arms of the anal sclerite (resulting in a subrectangular-shaped sclerite), but there is no evidence to suggest that this is in any way homologous with the arrangement found in *Twinnia* and *Gymnopais*. Indeed, the most plesiotypic species of *H.* (*Parahelodon*) has the hypothesized primitve type of anal sclerite for Prosimuliini (figs. 5, 9a).

Character 50.

Anal sclerite with anterodorsal arms borne on an elongate common stalk (= median sclerite), resulting in a Y-shaped structure. — The Y-shaped appearance of the anal sclerites of *Twinnia* and *Gymnopais* is largely owing to the form of the median sclerite. The median sclerite typically is in the form of a rectangular- or subrectangular-shaped plate that gives rise to the anterodorsal and posteroventral arms (figs. 9a, 9b) (**0**). In *Twinnia* and *Gymnopais* larvae, the median sclerite is considerably narrower and longer than the ones found in other Prosimuliini, with the effect of displacing the anterodorsal arms anteriorly (fig. 9d). No other simuliid that I am aware of has the anterodorsal arms situated so far anteriorly. Combined with the rudimentary form of the the posterodorsal arms (see discussion of character 49 above), the anal sclerite appears Y-shaped in dorsal view. This arrangement is clearly unique, and is strong evidence of the monophyly of *Twinnia* + *Gymnopais* (**1**).

3.1. Matrix of characters analyzed for evidence of monophyly and genus-group relationships of Prosimuliini.

TAXON/CHARACTER	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
PROSIMULIUM	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HELODON s.str.	0	0	0	0	1/2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PARAHELODON	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
DISTOSIMULIUM	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
UROSIMULIUM	0	0	0	0	1	0?	1	1	1	1	1	0	0	0	0	0	0	1	0	0
LEVITINA	0	1	0	0	1	0	2	2	0	0	1	1	1	1	1	1	1	2	1	1
TWINNIA	0	1	0	0	2	0	3	2′	0	0	0	2	2	1	1	1	1	3	1	1
GYMNOPAIS	0	0	0	0	2	0	2	2′	0	0	0	1	2	1	1	1	1	2	1	1

TAXON/CHARACTER	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
PROSIMULIUM	0	0	0	1″	0/1	0	0	0	0	0	0	0	0	0	0	0	0	0/1	0	0
HELODON s.str.	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1/2
PARAHELODON	1	0	0	0	0/1′	1	1	1	1	0	0	1	0	0	0	0	0	0/1/2	0	1
DISTOSIMULIUM	1	0	0	1″	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0	1
UROSIMULIUM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
LEVITINA	1	1	1	1′	1″	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1
TWINNIA	1	1	1	1′	1″	0	0	0	1	0	0	0	0	0	0	0	0	2	1	2
GYMNOPAIS	1	1	1	0	1″	0	0	0	1	0	1	0	0	0	0	0	0	2	1	2

TAXON/CHARACTER	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65
PROSIMULIUM	0	0	0	0	0	0	0	0	0/1	0	0	0	0	0	0	0	0/1	0	0	0
HELODON s.str.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PARAHELODON	0	0	0	0/1	0	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0
DISTOSIMULIUM	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0
UROSIMULIUM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LEVITINA	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1
TWINNIA	1	1	2	1	1	0	0	0	1	0	0	0	0	0	0	1	1	1	2	2
GYMNOPAIS	1	1	2	1	1	0	0	0	0/1	0	0	0	1	0	0	0	0	0	1	1

TAXON/CHARACTER	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81
PROSIMULIUM	0	0	0/1	0	0	0	0	0	0	0	0	0	0	0	0	0
HELODON s.str.	0	0	0/1	0	0	0	0	0	0	0	0	0	0	0	0	0
PARAHELODON	0	0	0/1	0	0	0	0	0	0	0	0	0	0	0	0	0
DISTOSIMULIUM	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
UROSIMULIUM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LEVITINA	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
TWINNIA	0	0	0/1	0	0	0	0	0	0	0	0	0	0	0	0	0
GYMNOPAIS	1′	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1

3.7.7 Summary

Monophyly of genus-groups of Prosimuliini

Analysis of external structural characters, including features of the male and female terminalia, provides evidence of the monophyly of the eight genus-group taxa recognized in Prosimuliini: *Prosimulium* Roubaud, *Helodon* Enderlein, *Parahelodon* Peterson, *Distosimulium* Peterson, *Urosimulium* Contini, *Levitinia* Chubareva & Petrova, *Twinnia* Stone & Jamnback, *Gymnopais* Stone. Monophyly in each instance is supported by 2 or more hypothesized synapotypies, of which at least one is apparently autapotypic. Because of homoplasy, the monophyly of *Helodon* remains tenuous — at least as defined by structural characters.

Cytological information provides evidence of the monophyly of five genus groups recognized in Prosimuliini *viz. Helodon, Parahelodon, Distosimulium, Twinnia,* and *Gymnopais* (Rothfels 1979). *Levitinia* and *Urosimulium* are known cytologically from only one species each, and so hypotheses about monophyly are derived from structural characters alone. The cytological transformation series of *Prosimulium s.str.* shows that five major lineages can be derived independently from the same standard sequence — the hypothetical "*Prosimulium* standard" (Rothfels *loc. cit.*, fig. 4). This same standard sequence gives rise to the "*Helodon* standard", which in turn gives rise to all the other genus groups of Prosimuliini. There is thus no single cytological feature that defines *Prosimulium s.str.*, exclusive of all other Prosimuliini. However, the monophyly of *Prosimulium* is clearly supported by four hypothesized structural synapotypies described under characters 6 - 9.

This combination of morphological and cytological information makes possible a reevaluation of currently held notions about prosimuliine genus-group definitions. Of all the definitions currently in use, Peterson's (1970, 1981) concept of Nearctic genus groups included in Prosimuliini most closely approximates the system adopted here, based on the world fauna. Most concepts of *Helodon s.str.* and *Prosimulium s.str.* have proven difficult to define — at least as inferred from the assemblages of species previously included under those names. In a system based on monophyletic lineages, males, females and larvae of all genus groups are readily distinguished. Pupae lack features that permit characterization of all genus groups, with only the segregates *Gymnopais*, *Twinnia* and *Levitinia* being distinguished reliably in that stage.

Relationships among genus-group taxa of Prosimuliini

Analysis of structural characters alone does not fully resolve phylogenetic relationships among the eight genus-group taxa included in Prosimuliini (fig. 1). The basic topology of the cladogram was generated using structural characters, which in turn provided the information necessary to "root" the cytological transformation series of Rothfels (1979) (fig. 2). This combination of morphological and cytological information was instrumental in reconstructing the phylogeny of the prosimuliine genera in figure 3.

The hypothesis of a close relationship among the fanless prosimuliine genera is almost universally agreed upon. *Gymnopais* and *Twinnia* have long been recognized as sharing an immediate common ancestry (*e.g.* Wood 1978), and the recently described *Levitinia* has been attributed to that line as well (Chubareva & Petrova 1981, Beaucournu-Saguez & Braverman 1987). Uemoto (1980) dismisses similarities between *Gymnopais* and *Twinnia* as the result of convergence, and ranks the latter as a subgenus of *Prosimulium s.lat.*, while retaining *Gymnopais* as a separate genus. However, his conclusions are based on the assumption that *Gymnopais* is the most primitive prosimuliine, and most of the features listed in common with *Twinnia* and *Prosimulium* are strictly symplesiotypic.

Twelve hypothesized synapotypies (characters 17-28) support the monophyly of the fanless Prosimuliini. *Levitinia* has been compared to both *Gymnopais* and *Twinnia*, but no definite conclusions about the relationships of these three genera have yet been adduced. Evidence presented here suggests that *Levitinia* is the sister taxon of *Gymnopais* and *Twinnia* together. The monophyly of this latter clade is supported by eight hypothesized synapotypies (characters 43 - 50). Two characters suggest a close relationship between *Levitinia* and *Gymnopais*, namely, lack of a connection between the terminal plate of the genital fork (= sternum 9) and tergum 9, and presence on the anteroventral surface of the larval mandible of a series of rows of spine-like scales (= apical mandibular brush). However, sheer weight of characters suggests that the first mentioned hypothesis is to be favored. Lack of a connection between the tergum and sternum of segment 9 is a regressive feature, and is therefore not convincing as a phylogenetic indicator. Shared presence of numerous rows of spine-like scales on the larval mandible is more problematic, as no such feature is evident in any other simuliid. I have suggested under the discussion of characters 63 and 64 that the form of the larval mandible is unique in *Twinnia*, and that the anteroventral margin of that structure is probably not brought into contact with the substrate (as it is in *Gymnopais*, and presumably *Levitinia* as well). It seems possible therefore that spine-like scales are in the groundplan of the entire clade, with subsequent loss or reduction in *Twinnia*. A single row of 3 or 4 spine-like scales on the *Twinnia* larval mandible lends credence to this hypothesis.

Cytological information confirms the monophyly of *Levitinia*, *Twinnia*, and *Gymnopais*, but apparently does not provide the resolution necessary to determine interrelationships among these segregates (Chubareva and Petrova 1981). These authors suggest that *Levitinia* occupies an "intermediate" position between *Gymnopais* and *Twinnia*, but failed to elaborate further. Unfortunately, the chromosome map published in that work is not of sufficiently high quality to draw any meaningful comparisons with chromosome maps prepared for *Gymnopais* and *Twinnia* (Rothfels, personal communication). A partially resolved cytological transformation series of Nearctic species of *Gymnopais* and *Twinnia*, and the relationship of these species to other Prosimuliini, has been published by Rothfels (1979).

The monophyly of *Helodon s.lat.* remains unsupported by external structural synapotypies, although the overall close relationship between included genus groups (*Helodon s.str.*, *Parahelodon*, *Distosimulium*) has not been questioned. Most of the similarities used suggest relationships are apparently symplesiotypic, and cannot be accepted in a cladistic system. Evidence for the monophyly of *Helodon s.lat.* is therefore based on purely cytological grounds. Members of *Helodon s.lat.* are defined by having fixed inversions IIIL-1 and 1xIIS, and floating inversion IIIS-3 (Rothfels & Freeman 1966, Rothfels 1979) (fig. 2).

If cytological information is accepted as evidence of the monophyly of *Helodon s.lat.* (and all available information indicates that chromosomal information is a powerful indicator of relationship), this provides the basis for more fully resolving relationships among included genus groups. There is a well supported sister group relationship between *Parahelodon* and *Distosimulium*, based on four hypothesized synapotypies (characters 31-34), and these two aggregates together are hypothesized to be the sister group of *Helodon s.str.* This set of relationships is fully corroborated by chromosomal evidence (Rothfels *loc. cit.*) (fig. 2). The arrangement of hypostomal teeth in larvae of *Parahelodon* and

Distosimulium is similar to the condition in fanless prosimuliines (*Levitinia, Twinnia, Gymnopais*). The median hypostomal tooth in both groups is characteristically very short, with its apex not extended anteriorly beyond the apex of the shortest lateral or sublateral tooth. Although this state is hypothesized to be apotypic for Prosimuliini, there is little evidence to suggest a close relationship between the fanless black flies and *Parahelodon* + *Distosimulium*. The hypostomae of fanless black flies have an array of specializations that adapts them for scraping algae and other organic matter from the substrate, and are readily distiguishable from the hypostomae of other Prosimuliini (see characters 25 and 26). It therefore seems possible that a short median tooth has been evolved independently at least twice in Prosimuliini.

The foregoing discussion has established that two major monophyletic groups can be recognized within Prosimuliini — the fanless Prosimuliini (*Levitinia* + *Twinnia* + *Gymnopais*), and *Helodon s.lat.* (*Helodon s.str.* + *Parahelodon* + *Distosimulium*). What is the relationship of these two lineages to each other, and to the remaining two genus-groups of Prosimuliini (*Prosimulium*, *Urosimulium*)? Evidence presented under the discussion of character 10 suggests that presence of a distinct basal or subbasal tooth on the female tarsal claw is a groundplan apotypy of the fanless Prosimuliini + *Helodon s.lat.* However, the character is subject to homoplasy, apparently having been evolved and lost several times independently in Simuliidae. Indeed, if a toothed female claw is ascribed to the groundplan of the fanless Prosimuliini + *Helodon s.lat.*, then the condition must have been lost at least twice in that clade — once in *Twinnia* + *Gymnopais*, and one or more times in *Helodon s.str.* (relationships among of *Helodon s.str.* species are not well enough resolved to determine how many times the tooth has been lost in that lineage). However, as indicated by Shewell (1955,1958), the toothed claw seems to have group significance, apparently being related to the ornithophilic habit of adult females. Females that have reverted to blood feeding upon mammals (*Twinnia* in part), or that have become autogenous (*Gymnopais*, *Twinnia* in part, *Helodon* in part), are apparently subject to losing the toothed condition.

Although the monophyly of the fanless Prosimuliini + *Helodon s.lat.* is only weakly supported by structural characters, there is strong cytological evidence to indicate the recent common ancestory of these two lineages. "*Helodon* standard", the hypothetical central sequence from which both lineages are derived, is distinguished from "*Prosimulium* standard" by fixed inversion IIIS-2, and by floating inversion IIIS-3 (fig. 2). Furthermore, members for which cytological information is available all share a basic inversion in IIIL (Rothfels and Freeman 1966, Rothfels 1979).

The monophyly of the largest single clade of Prosimuliini, *Prosimuium s.str.*, is strongly supported by four hypothesized synapotypies (characters 6 - 9). Three of the four synapotypies are unique among Prosimuliini, with one of these (character 9) being unique among Simuliidae. Because females of *Prosimulium s.str.* lack a basal or subbasal tooth on their tarsal claw, and none are known to blood-feed upon birds, it is suggested that this monophyletic assemblage forms the sister taxon of all other Prosimuliini. Unfortunately, cytological information does not provide a single common inversion that could be construed as a synapotypy of *Prosimulium s.str.* Instead, the *Prosimulium* standard sequence is shown to give rise to five independently derived lineages of *Prosimulium s.lat.* (and also to the *Helodon* standard, which ultimately gives rise to all other Prosimuliini cytologically examined)(cf. Rothfels 1979 fig. 4). Cytological information by itself neither corroborates nor refutes the hypothesis of a sister group relationship between *Prosimulium* and all other Prosimuliini. However, if we accept the four external structural synapotypies as strong phylogenetic evidence, and join together the cytologically "independently" derived lineages of *Prosimulium s.str.*, the resulting "rooted" cytophylogeny shows a clear sister group relationship between that taxon and all other Prosimuliini.

The only genus group that has not been considered so far is the enigmatic *Urosimulium*. Relationships of this well-defined monophyletic assemblage (characters 14 - 16) have remained unresolved since its discovery in 1963. Rothfels (1979) suggested that there might be cytological grounds for including *Urosimulium stefanii* (= *aculeatum* Rivosecchi) among the Palaearctic *Prosimulium s.str.* "*hirtipes* group". The problem with this interpretation is that *Urosimulium* shares none of the apotypies hypothesized for *Prosimulium*, and instead has the single structural apotypy hypothesized for Prosimuliini, exclusive of *Prosimulium*. I can only assume that Rothfels' conclusions are based on a survey of chromosomal maps provided by Frizzi *et al.* (1970), which are insufficiently clear to draw any definite conclusions about the relationships of *Urosimulium* (P. H. Adler, personal communication).

Based on over all phenetic similarities it is tempting to include *Urosimulium* among members of *Helodon s.lat.* However, as indicated above, there are no apparent structural characters that can be interpreted as a synapotypy of that lineage (either with or without *Urosimulium*). In the absence of convincing cytological information, the hypothesis of a close relationship between *Urosimulium* and *Helodon s.lat.* can not be rejected solely on the basis of lack of shared structural apotypies. Apparent striking differences between the immature stages of *Urosimulium* and the fanless Prosimuliini might inhibit some from suggesting a close relationship between these two groups. Nevertheless, characters 12-13 are here proposed as as possible synapotypies. Shared presence of a modified apical brush (character 12) is a tenuous synapotypy because features of the larval mandible have not been widely surveyed in Prosimuliini. The other hypothesized synapotypy, presence of a supernumerary arm projecting posteriorly from the anal sclerite (character 13), seems more promising, but I have had to draw some of my conclusions from illustrations in the literature (Contini 1963, 1966; Rivosecchi 1963, Bernard *et al.* 1972). The hypothesis of monophyly of *Urosimulium* + the fanless Prosimuliini is tentatively accepted until a more strongly corroborated hypothesis is adduced.

3.8 Classification

The monophyly and sister-group relationships of Prosimuliini genus groups is reasonably well established based on structural grounds. Cytological information corroborates most of the hypothesized relationships, and provides resolution of what would otherwise have remained an unresolved trichotomy in Prosimuliini, exclusive of *Prosimulium s.str.* Given the close agreement between morphologically- and cytologically-derived cladograms, it seems desirable to forward a reclassification of Prosimuliini based on the hypothesized relationships.

There has not been a serious attempt to classify Simuliidae based on a comprehensive hypothesis of phylogenetic relationship. Despite claims to the contrary, Rubtsov's (1974) classification is really not founded on phylogenetic relationship at all, but is rather a compilation of branching diagrams illustrating preconceived notions about relationship. As in most systems proposed to date, genera or groups of genera are arranged according to perceived morphological discontinuities between them. Thus, relatively aberrant groups of species, such as those belonging to the fanless Prosimuliini, are accorded relatively high taxonomic rank, despite the fact they belong to the most derivative lineage of Prosimuliini. In a phylogenetic system, such species could be ranked only at the level of other segregates in that clade (Wood 1978). Accordingly, distantly related species might be included in the same segregate, because they look similar on overall balance of characters. The problem with viewing all character states simultaneously (and with equal weight) is that the majority are plesiotypic, and cannot be relied upon to demonstrate relationship. Classifications based on a dialectical or non-cladistic approach to systematics are less informative than ones based on cladistic relationships because (a) they do not accurately reflect relationships among included segregates, and (b) often recognize non-monophyletic assemblages of species.

In formulating a classification of Prosimuliini, one must take into account different philosophies concerning the ranking of supraspecific aggregates. Rubtsov's (1974) system recognizes a large number of relatively small genera; whereas Crosskey's (1981,1987) classifications recognize fewer, larger, genera, of which the largest are divided into a number of subgenera. If a classification of Simuliidae is to be balanced relative to other Diptera, and in particular with other families of Culicomorpha, it is clear that a conservative approach is to be favored. This is particularly true if the structural homogeneity of black flies is to be taken into consideration.

One possible approach would be to recognize only a single genus in Prosimuliini, namely, *Prosimulium* Roubaud. The eight genus-groups could then all be ranked at the subgeneric level. The problems with this approach are (a) there is no indication about how the subgenera are related to one another, and (b), as already indicated by Wood (1978), phenetic differences between the fanless black flies and other Prosimuliini would inhibit many workers from ranking these segregates as subgenera of *Prosimulium*. The insistence of many workers that members of the fanless Prosimuliini should be accorded an especially high rank is not entirely justified. First-instar larvae of Prosimuliini are all effectively fanless, and the various genus groups that have been examined are virtually indistiguishable in that stage (Craig 1974). Unlike other simuliids that have well-developed fans in the first instar, the prosimuliine fan (when present) does not become expressed until the second instar. The apparently aberrant condition of larvae of *Levitinia*, *Twinnia*, and *Gymnopais* is no more than neotenic retention of the fanless state through second- and later instars (Wood 1978). Recent discovery of adults and pupae of *Levitinia* reduces even further the apparent distinctiveness of members of that clade. *Levitinia* adults are even more similar to *Prosimulium s.lat.* than to *Twinnia* adults, and so the "gap" between the fanless black flies and other prosimuliines is lessened further still. Should *Urosimulium* eventually prove to be the well-corroborated sister taxon of the fanless black flies, I suggest that there would be no significant structural gap, and that it would be impossible justify the special status traditionally given to members of the group. It is interesting to note that it has not been found necessary to give special status to the fanless Tahitian simuliids (*oviceps* Edwards, *neoviceps* Craig), which have been included with their fanned relatives in the *Simulium* subgenus *Inseliellum* Rubtsov (Craig 1987).

These comments not withstanding, I have attempted to adopt a classification acceptable to the largest number of workers, but reflecting phylogenetic relationships as indicated in figure 3. The problem with this approach is that a larger number of genera will have to be recognized in what is otherwise an extremely homogeneous assemblage of black flies. *Levitinia*, *Twinnia*, and *Gymnopais* are all ranked at the generic level, as are the segregates *Prosimulium s.str.* and *Urosimulium*. *Helodon s.str.*, *Parahelodon* and *Distosimulium* are all ranked as subgenera of *Helodon s.lat.*, in accordance with the opinion of Rothfels (1979) that they are cytologically derived from an immediate common ancestor. With the possible exceptions of *Helodon s.lat.* and *Prosimulium s.str.*, the generic concepts proposed in the present work are widely used already. In many respects, it bridges the gap between the two systems currently in use (Rubtsov 1974; Crosskey 1981, 1987).

Although there are sufficient grounds for uniting the fanless Prosimuliini into a single genus (*Gymnopais*), I believe that most workers prefer to maintain *Levitinia* and *Twinnia* as separate genera (Wood 1978, Crosskey 1981, 1987). *Urosimulium* will have to be ranked as a full genus as long as the hypothesis of a sister group relationship with the fanless Prosimuliini is upheld. Future work may possibly reveal that *Urosimulium* is best assigned to *Helodon s.lat.*, whereupon it should be relegated to that genus in subgeneric status. The genus *Prosimulium* is the large segregate of Prosimuliini, consisting of a number of clearly-defined, monophyletic lineages (Rothfels 1979). However, there may not be sufficient structural difference between members of these lineages to warrent their subgeneric recognition. This is an area requiring further study.

Appendix 1 is a list of the world species of Prosimuliini arranged under the system described above.

3.9 Zoogeographic Considerations

Present-day distributional patterns of Prosimuliini genus groups are , in themselves, not sufficiently illuminating to undertake a comprehensive zoogeographical analysis. Simply not enough is known about relationships within each of the lineages to determine possible geographical sources of origin, and subsequent vicariant events or routes of dispersal. Comments are therefore restricted to general observations about present-day patterns.

The fanless prosimuliines are widely distributed in the Holarctic region, although the majority are situated in the eastern Palaearctic region. The genus *Levitinia,* which is hypothesized to be the most plesiotypic member of fanless Prosimuliini, is apparently the most restricted in terms of its known range. However, *Levitinia* has been known to science only during the present decade, and so it is possible that extralimital records will be discovered. The two described species, *Levitinia freidbergi* and *L. tacobi,* are known from mountainous areas of Israel (Golan Heights) and Tadzhikistan (USSR, Pamir Mountains) respectively. This is suggestive of a relict distribution, because there are no apparent similarities between the faunas of these two regions. Perhaps the genus was once more widely distributed in mountains of the southern Palaearctic region.

Members of *Gymnopais* are distributed farther east than *Levitinia*, their western-most limits being the the Altai mountains of western Siberia. In effect, the Tien Shan Mountians seem to form a barrier between *Gymnopais* and *Levitinia*, for I am aware of no records of either segregate from that region. Whether this "barrier" is real, or is merely a collecting artifact, cannot be determined given present evidence. There are no apparent barriers between the Pamirs and the Tien Shan mountains, and so one might expect to find

Levitinia in the latter region as well. Perhaps it is the dry-steppe corridors (Dzungarian Gates) between the Tien Shan and Altai mountains that serve as a present-day barrier.

From the Altai, *Gymnopais* species are widely encountered in mountainous regions of Asia, east to Kamtchatka. The most southerly record known to me is from Primorye, presumably from the Sichote-Alin mountains north of Vladivostok (~44°N) (Bodrova 1975). The northern limit of Palaearctic *Gymnopais* is unknown to me, although I would expect that species would be found in the Chukchi peninsula (= Beringia, in part).

The five endemic Nearctic species of *Gymnopais* are centered mainly in unglaciated regions of Alaska and the Yukon Territory (= Beringia, in part). Three of these species are bisexual, and have apparantly been unable to disperse out of Beringia following retreat of Wisconsinin ice (Wood 1978). The two other species, both parthenogenetic (Rothfels 1979), are much more widely distributed than their sexual counterparts. One of these species, *G. holopticoides* Wood, is distributed from Beringia east across the southern arctic islands to Labrador; the other species, *G. dichopticoides* Wood, is distributed from Beringia south along the Rocky Mountians to southern Alberta. Perhaps their freedom from the neccessity to mate permitted the parthenogenetic forms to disperse more easily than their sexual relatives.

I have suggested that water courses formed between the retreating ice sheets may have provided a route by which the parthenogenetic forms could have obtained their present-day distribution (Currie, unpublished). Adults of neither species are capable of flight, and so it seems more likely that dispersal was effected in the larval stage. In the north, I have hypothesized that *G. holopticoides* has dispersed along water courses that must have formed between the Inuitian ice sheet[11] and the northern edge of Laurentide ice.

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[11] England (1976) suggested that arctic ice was not coalesced into a single large ice sheet, but was rather comprised of a number of smaller caps of ice, each of which were centred

This might explain why such a poorly dispersing black fly is presently located on Victoria and Banks Islands (both of which are presently widely separated from the adjacent mainland). In the south, I have hypothesized that *G. dichopticoides* dispersed along watercourses that must have formed between the Cordilleran ice sheet and the western edge of Laurentide ice. An ice-free corridor between the two ice sheets is known to have persisted along the front ranges of the Canadian Rocky Mountains during late Wisconsinin times (Matthews 1979). This corridor originated in Beringia, and extended ever farther south as the climate ameliorated. This would have provided a route by which larvae could have dispersed easily. It is interesting to note that the most southerly representatives of *G. dichopticoides* are either restricted to streams that originate at the bases of glaciers (actually remnants of Wisconsinin ice), or to headwaters of permanent, high-alpine streams (personal observation).

To test the hypothesis that *G. dichopticoides* could have achieved their southern limit via a Rocky Mountain front-range corridor, I examined a number of suitable habitats west of the Rocky Mountains. By suitable I mean water courses that take their sources from areas of permanent or semi-permanent ice, such as glaciers. The hypothesis would be falsified if any population of *Gymnopais* were found in the interior ranges of British Columbia. Glacial streams in the following mountain ranges were examined for the presence of *Gymnopais*: Cariboo Mountains, Selkirk Mountains, Purcell Mountains, and southern Coast Mountains. Since none of the numerous streams sampled yielded any specimens of *G. dichopticoides* (nor any other member of that genus), I was unable to refute the hypothesis of a Rocky Mountain front-range dispersal route during late Wisconsinin times.

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on individual arctic islands. Either model of ice distribution can be used to explain the presence of postglacial water courses between the northern mainland, and the Canadian arctic archipelago.

The third genus of fanless Prosimuliini, *Twinnia*, is widely distributed throughout the northern forests of Eurasia and North America. Unlike members of *Gymnopais* and *Levitinia*, species of *Twinnia* are not restricted to high elevation- or high latitude environments. Instead, apparently they require only the type of conditions that give rise to permanent or semi-permanent springs (typically hilly or high relief terrain) (Wood 1978). Relationships between the described species are so inadequately understood that it is impossible to discuss present-day distributions in a zoogeographic framework. It is worthy to note, however, that there seems to be an affinity between some of the Japanese species (esp. *T. japonensis* Rubtsov), and those occurring in western North America (*T. nova* (Dyar & Shannon), *T. hirticornis* Wood).

The three fanless genera of Prosimuliini are effectively allopatric in their distribution. Both species of *Levitinia* are geographically well removed from their nearest relatives in *Gymnopais* and *Twinnia*. Members of these latter two genera, although occupying the same gross geographical regions of the Holarctic, are clearly separated altitudinally where they occur together (Wood 1978, personal observation).

Members of the genus *Urosimulium* have one of the most intriguing distributions among Prosimuliini. Included species are apparently restricted to only a few, high - elevational localities in the western Mediterranean. In the absence of any records of *Urosimulium* from the mountains of Spain, I can interpret their present-day distribution only as being relict. The mountains in which they now live either formed part of the shores of, or were islands in, the Tethys sea. Perhaps we are now left with a few surviving relicts of what was once a more wide-spread and diverse assemblage.

In Section 3.7.3 on relationships among genus-group taxa, I suggested that there may be a sister-group relationship between *Urosimulium* and the fanless prosimuliines. If the hypothesized set of relationships are accepted as diagrammed in fig. 3, and if the genera are substituted for the areas in which they occur, then an "area cladogram" can be generated (*e.g.* Rosen 1976). The resulting area cladogram suggests that the progenitor of the assemblage might have originated in the western Palaearctic region, and that diversification into various lineages has occurred farther east. Hence, the most plesiotypic member of the lineage (*Urosimulium*) is centred in the western Mediterranean, followed by the next most plesiotypic lineage (*Levitinia*) in the Middle East and Soviet central Asia, followed by the more derivative lineages (*Twinnia* and *Gymnopais*) centered in the northern forests and far-eastern mountains respectively.

The generality of an area cladogram can be examined by comparison with other unrelated groups endemic to the areas under consideration (Humphries and Parenti 1986). Corroboration of a particular pattern might lead eventually to a general statement about the relative recent ancestry of the biotas under consideration. No other taxa that I am aware of show the same pattern as described above, and so the utility of the area cladogram, at least insofar as providing a well corroborated series of vicariance hypotheses, is not realized in this instance. Extinction, dispersal of widespread taxa, and restricted distributions of taxonomic groups may all lead to incongruence in the general area cladogram (Humphries and Parenti *loc.cit.*). Simuliids have tremendous dispersal capabilities, and I have already suggested that distribution of some of the genera under consideration is relict. It is possible therefore that black flies are not useful models for this type of investigation.

Members of the genus *Helodon s.lat.* are widely distributed throughout the Holarctic region. As with most other Prosimuliini, patterns attributable to vicariance may be obscured by the fact that adults are generally strong flyers. Moreover, females of this segregate typically possess a distinct basal or subbasal tooth on the tarsal claw, which is an adaptation for clinging to the plumage of their avian hosts. The possibility that gravid females have been carried long distances cannot be dismissed. *Helodon* (*Parahelodon*) members comprise the most narrowly distributed segregate, occurring only in the northern forests of the Nearctic region; *Helodon* (*Distosimulium*) members also have a transcontinental distribution in North America, but are also known from Japan. By far the largest- and most wide spread segregate is *Helodon s.str.*, which occurs throughout the Palaearctic- and western Nearctic regions. This latter group has an interesting distribution inasmuch as the single largest concentration of described species is in Siberia. There is an apparent large disjunction between the Siberian species, and those occurring in the western Palaearctic region *viz. H. rufus* (Meigen) (Scandinavia, northwestern USSR), *H. maruashvili* (Machavariani) (Transcaucasia), and *H. laamii* (Beaucournu-Saguez & Bailly-Choumara) (Morocco). If this is truely indicative of the distribution of *Helodon s.str.*, and not merely a collecting artifact, it would then seem reasonable to suppose that the three western species are relicts of what was a formerly wide-spread distribution.

Prosimulium s.str. members are the most widely distributed prosimuliine segregate, including the most northerly record for Simuliidae (Bjørnøya, 74° 25′ N). The genus apparently differentiated very early, as judged from its hypothesized sister-group relationship with all other Prosimuliini. Little else can be inferred about the zoogeographic history of *Prosimulium s.str.*, as intrageneric relationships remain inadequately understood.

Figure 1. Cladogram showing hypothesized relationships of genus-group taxa of Prosimuliini, based on structural characters alone.

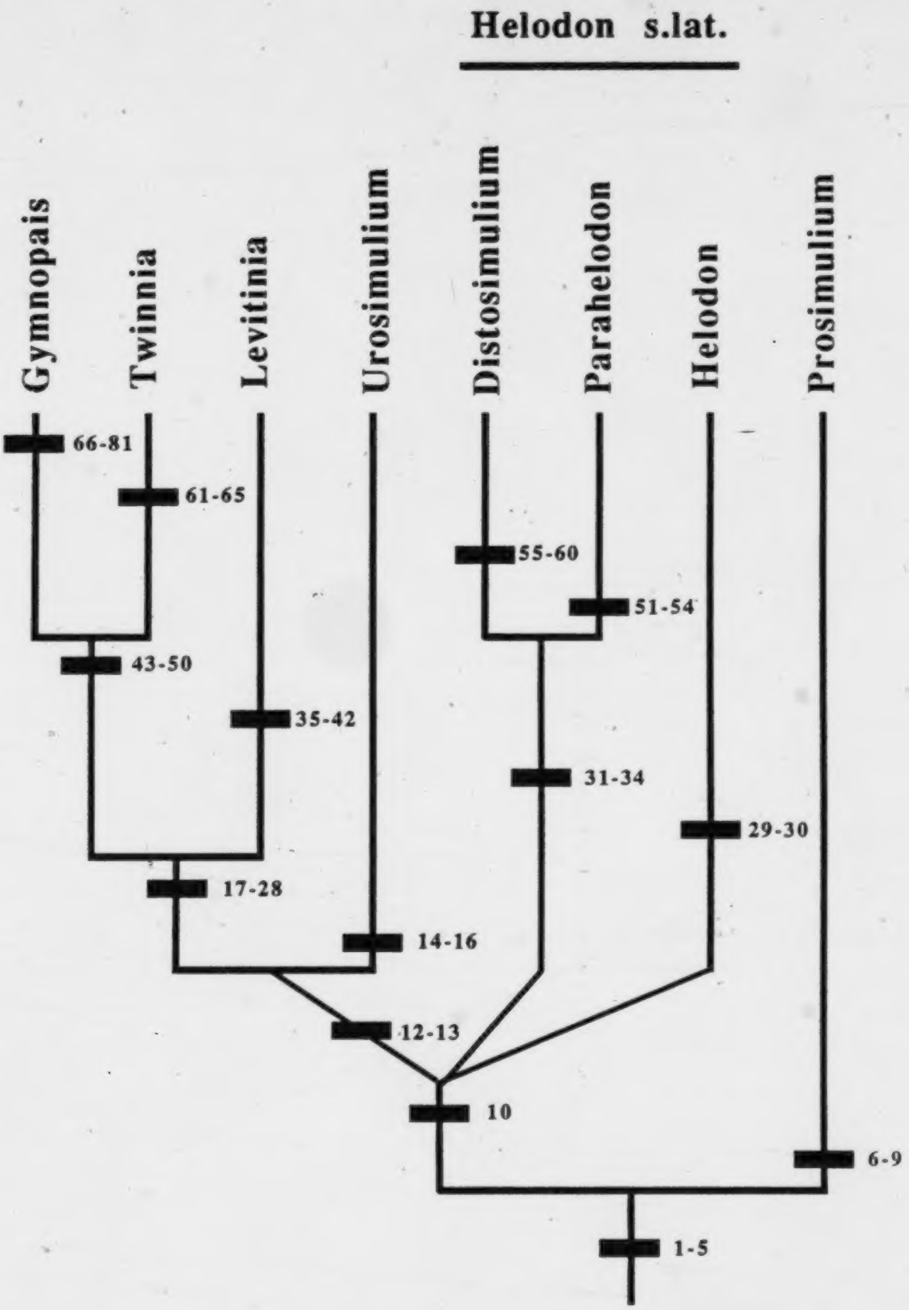

Helodon s.lat.
Gymnopais
Twinnia
Levitinia
Urosimulium
Distosimulium
Parahelodon
Helodon
Prosimulium
66-81
61-65
55-60
51-54
43-50
35-42
31-34
29-30
17-28
14-16
12-13
10
6-9
1-5

Figure 2. Cytophylogeny of genus-group taxa derived from "*Helodon* standard" and "*Twinnia* standard", as discussed in text (redrawn from Rothfels 1979). Underlined symbols on connecting lines show fixed changes like inversions, coded by numbers from chromosomes (I-III) and arms (S vs. L), or interchanges, as in IIS+IIIS. Symbols in brackets show floating inversions. "NO transp." denotes change in position of nucleolar organizer. The origin of the cytophylogeny is arbitrary, chosen on the basis of its centrality (*i.e.* it exists as such in a considerable number of Prosimuliini species, and gives rise to the largest number of independantly derived lineages). Inversion symbols read from the origin are additive. The fate of floating inversions is indicated following a branch point (carried floating, becoming fixed, or dropped). *Prosimulium* standard is the origin, and the diagram should be read from that point.

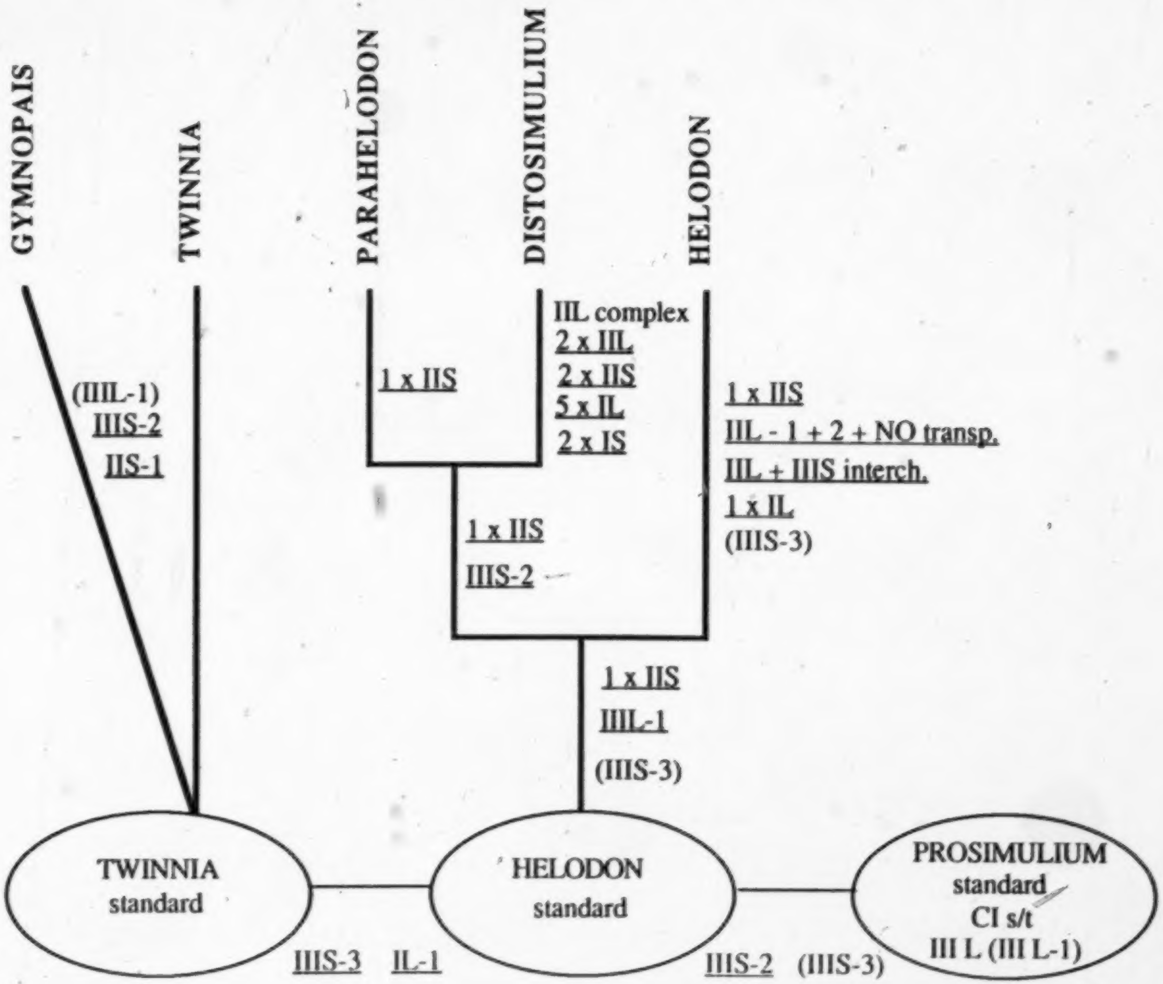
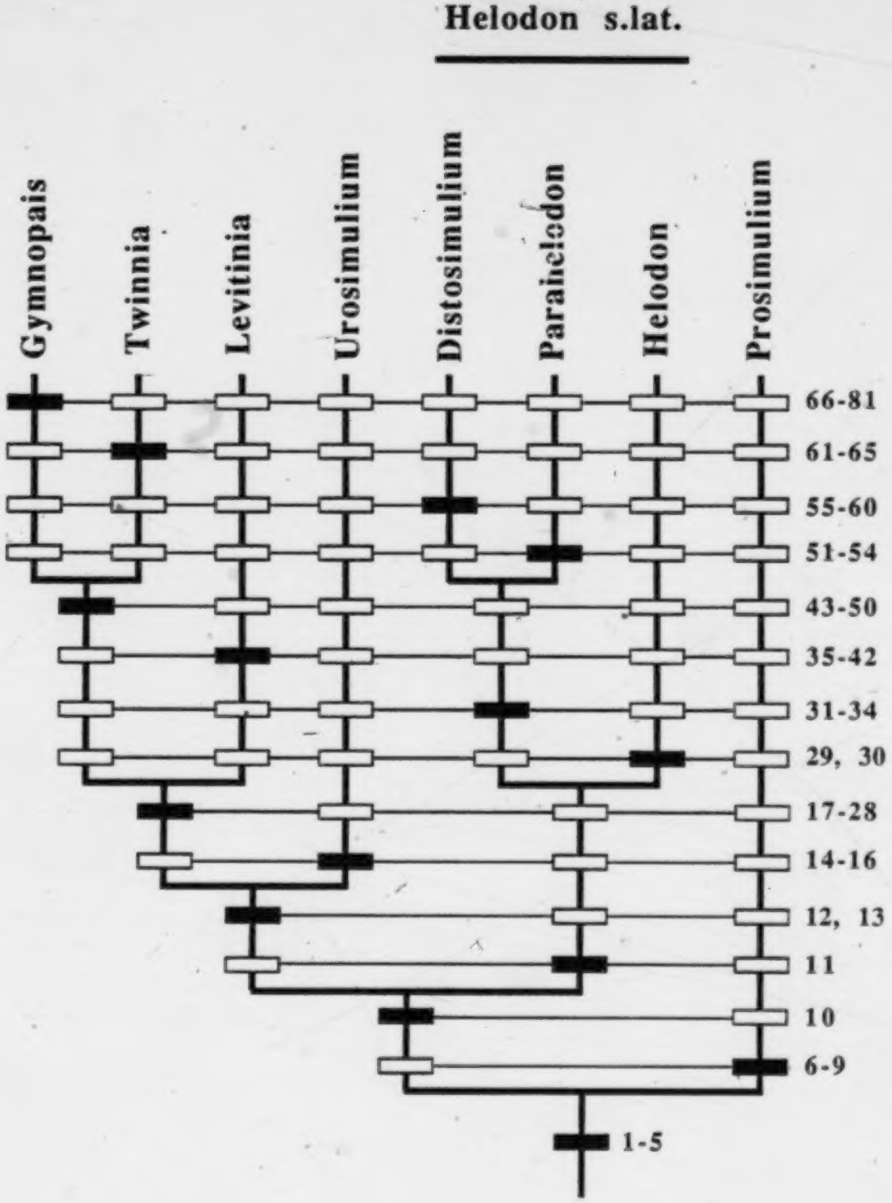
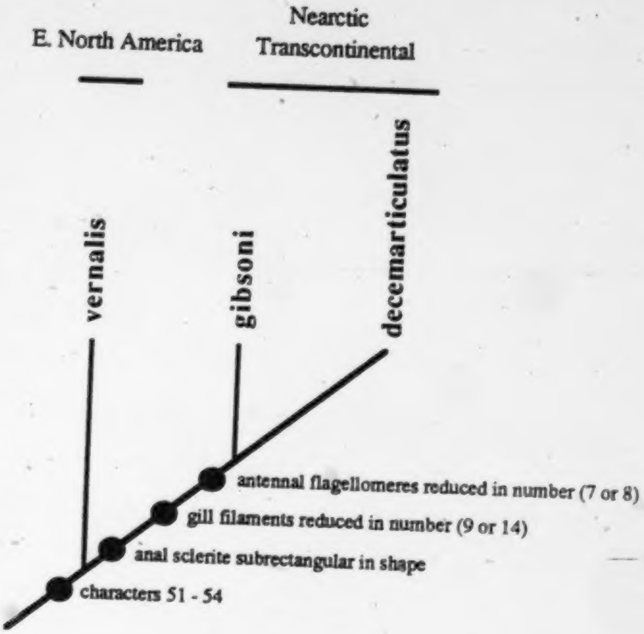

GYMNOPAIS
TWINNIA
PARAHELODON
DISTOSIMULIUM
HELODON
(IIIL-1)
IIIS-2
IIS-1
1 x IIS
IIL complex
2 x IIL
2 x IIS
5 x IL
2 x IS
1 x IIS
IIL - 1 + 2 + NO transp.
IIL + IIIS interch.
1 x IL
(IIIS-3)
1 x IIS
IIIS-2
1 x IIS
IIIL-1
(IIIS-3)
TWINNIA
standard
HELODON
standard
PROSIMULIUM
standard
CI s/t
III L (III L-1)
IIIS-3
IL-1
IIIS-2
(IIIS-3)

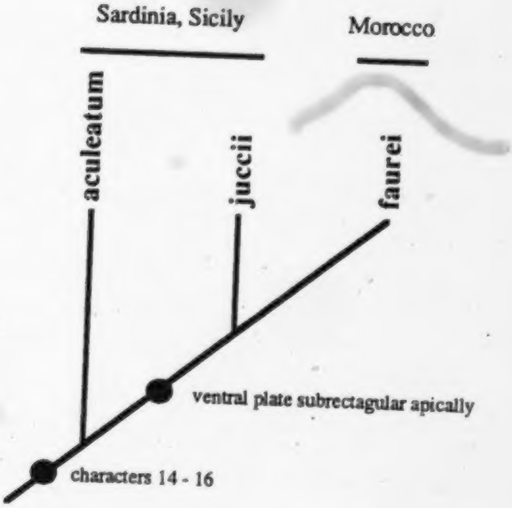
Figure 3. Cladogram showing hypothesized relationships of genus-group taxa of Prosimuliini, based on structural and cytological characters.


Helodon s.lat.
Gymnopais
Twinnia
Levitinia
Urosimulium
Distosimulium
Parahelodon
Helodon
Prosimulium
66-81
61-65
55-60
51-54
43-50
35-42
31-34
29, 30
17-28
14-16
12, 13
11
10
6-9
1-5

Figures 4 - 5. Relationships among species of *Helodon (Parahelodon)* Peterson and *Urosimulium* Contini: (4) cladogram showing hypothesized relationships of species of *Helodon (Parahelodon)* Peterson; (5) cladogram showing hypothesized relationships of species of *Urosimulium* Contini.


E. North America
Nearctic Transcontinental
vernalis
gibsoni
decemarticulatus
antennal flagellomeres reduced in number (7 or 8)
gill filaments reduced in number (9 or 14)
anal sclerite subrectangular in shape
characters 51 - 54

4


Sardinia, Sicily
Morocco
aculeatum
juccii
faurei
ventral plate subrectagular apically
characters 14 - 16

5

Figure 6. Hypothesized transformations of the Prosimuliini pupal pleuron, as discussed in text (diagrammatic representation of left side of abdomen; segments 3 - 9).

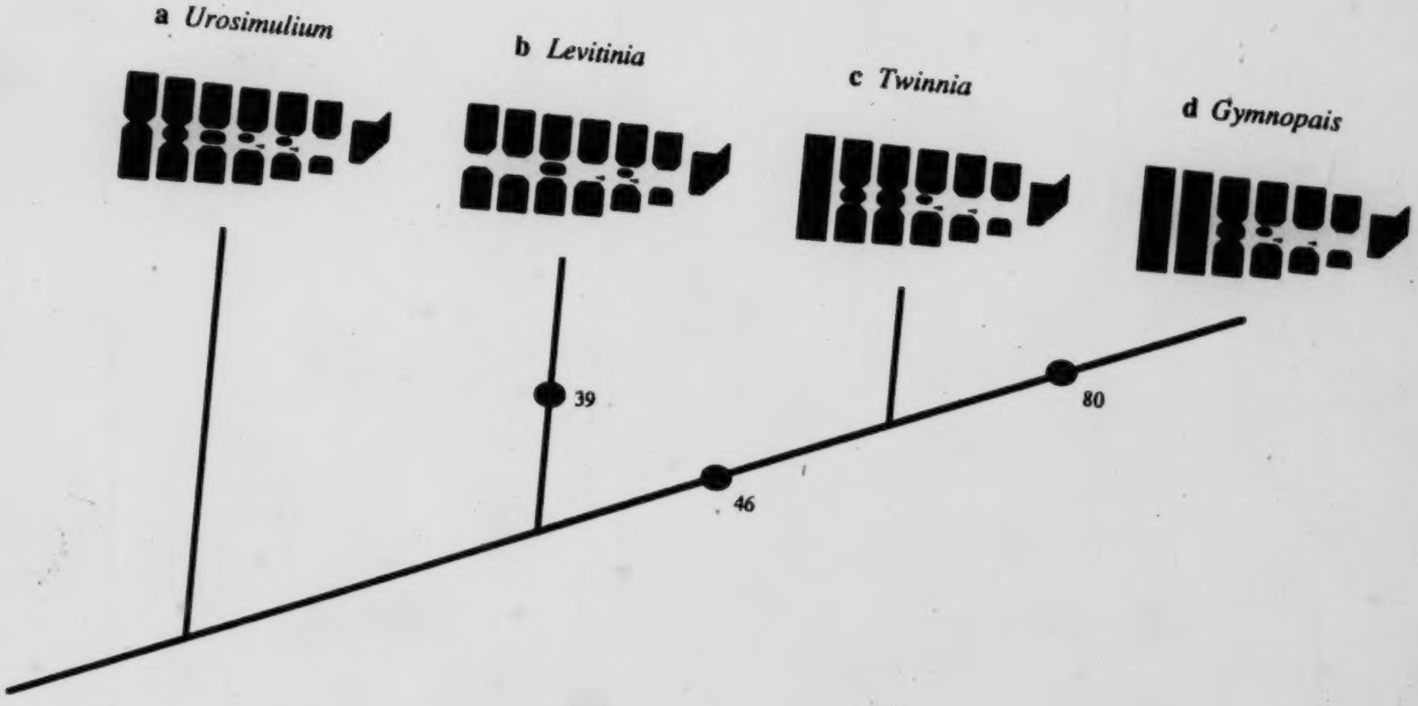

a Urosimulium
b Levitinia
c Twinnia
d Gymnopais
39
46
80

Figure 7. Hypothesized transformations of the Prosimuliini pupal abdominal tergum, as discussed in text (diagrammatic).

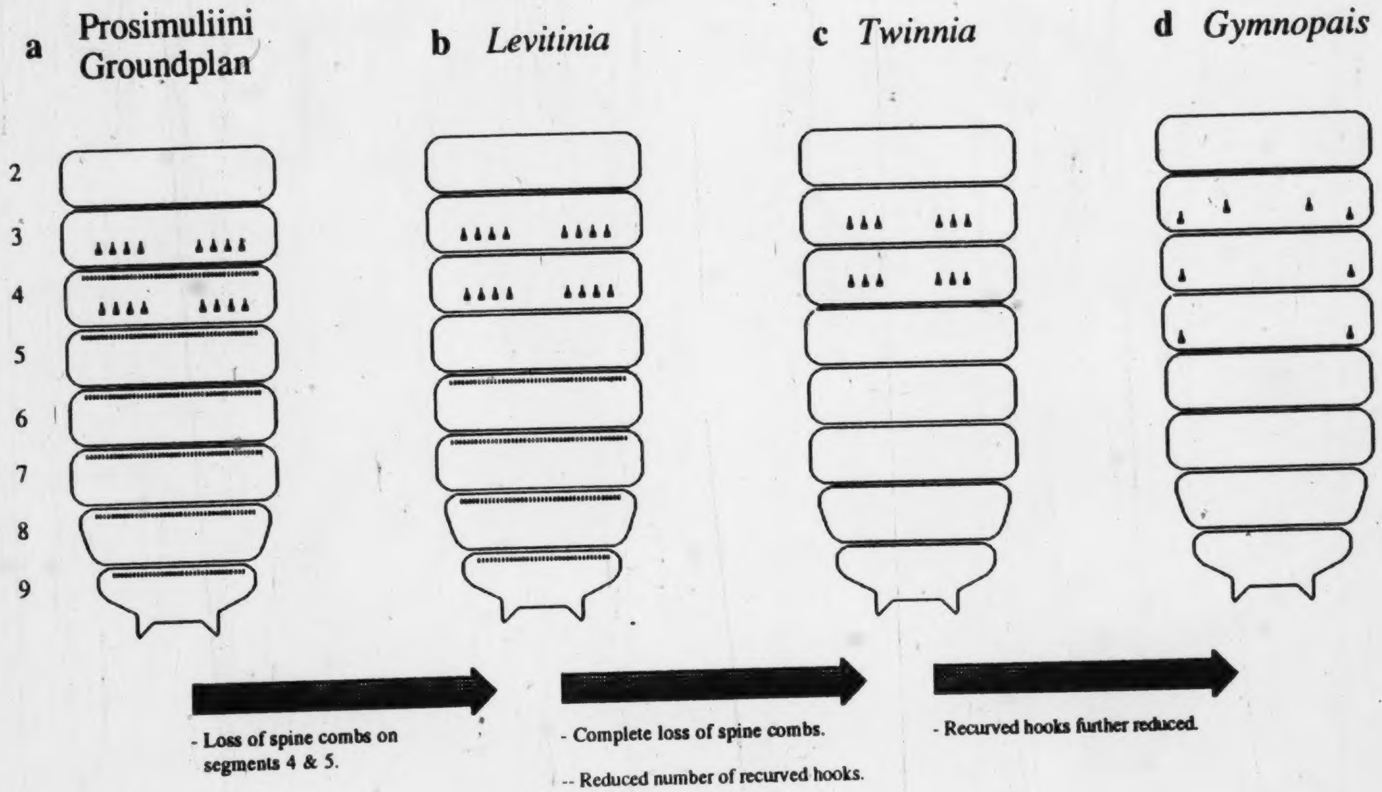

a Prosimuliini Groundplan
b Levitinia
c Twinnia
d Gymnopais
2
3
4
5
6
7
8
9
- Loss of spine combs on segments 4 & 5.
- Complete loss of spine combs.
-- Reduced number of recurved hooks.
- Recurved hooks further reduced.

Figure 8. Arrangement of recurved hooks on the Prosimuliini pupal abdominal sternum, as discussed in text (diagrammatic).

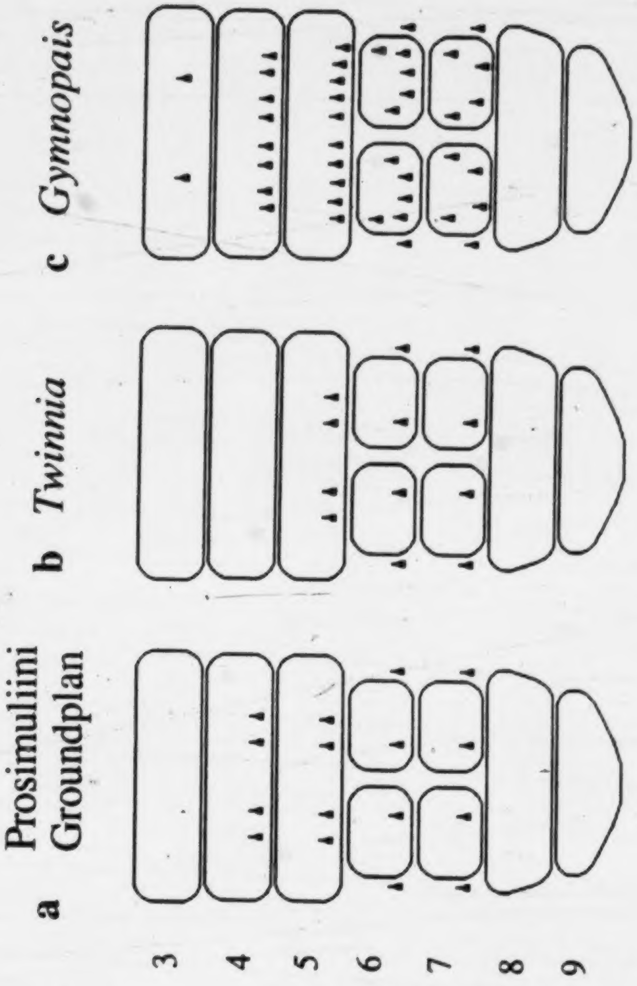
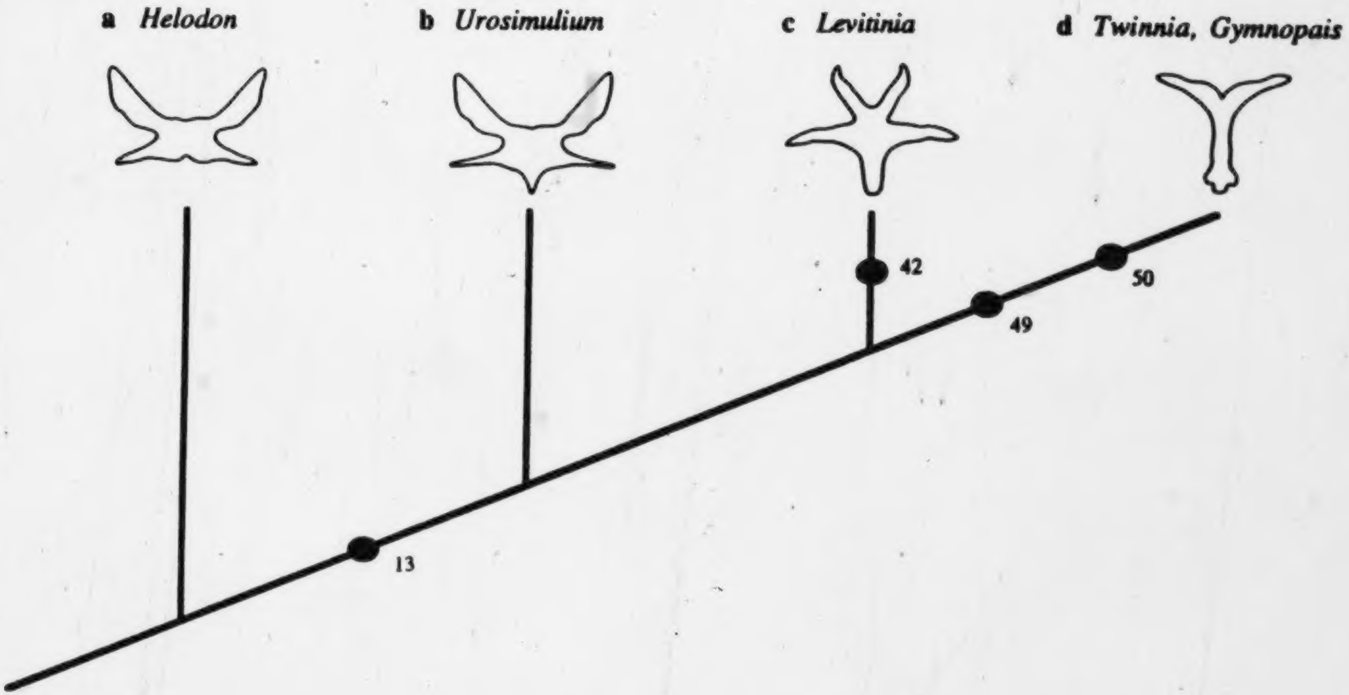

a
Prosimuliini
Groundplan
b
Twinnia
c
Gymnopais
3
4
5
6
7
8
9

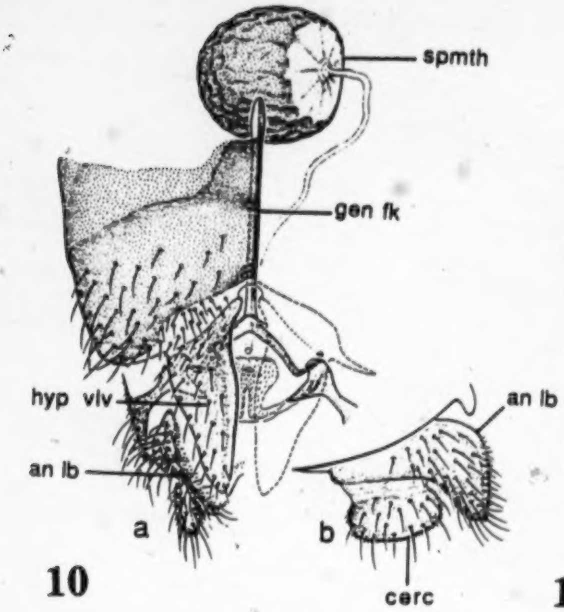
Figure 9. Hypothesized transformations of the Prosimuliini anal sclerite, as discussed in text (semi-diagrammatic).


a Helodon
b Urosimulium
c Levitinia
d Twinnia, Gymnopais
42
50
49
13

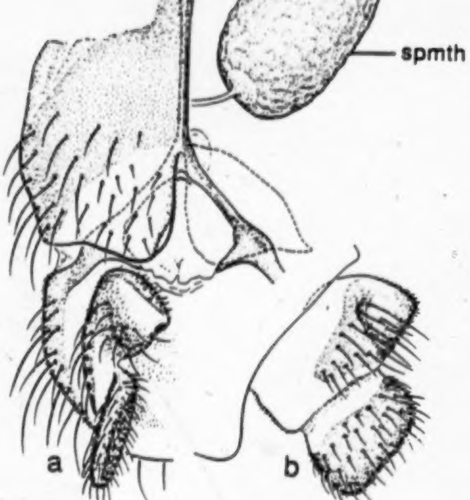
Figures 10 - 13. Female terminalia (a , ventral view with left hypogynial valve removed; b, right lateral view at right angles to plane of ventral view) of (10) *Prosimulium mixtum* Syme & Davies; (11) *Helodon* (*Helodon*) *onychodactylus* (Dyar & Shannon) complex; (12) *H.* (*Parahelodon*) *decemarticulatus* (Twinn); (13) *H.* (*Distosimulium*) *pleuralis* (Malloch).

Abbreviations: an lb = anal lobe; cerc = cercus; gen fk = genital fork; hyp vlv = hypogynial valve; spmth = spermatheca; st = sternum; tm plt = terminal plate.

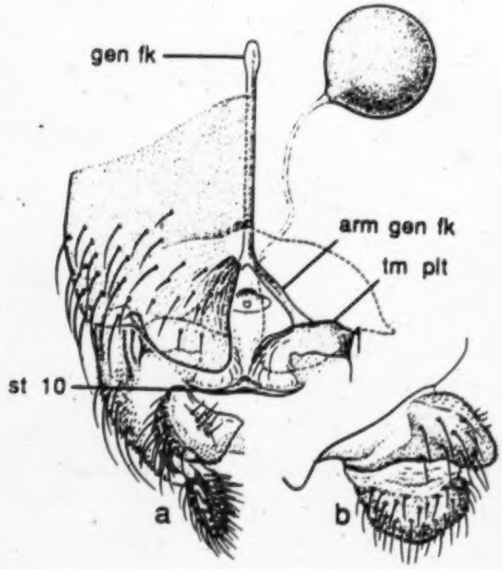
(Figures reproduced from McAlpine, J. F. *et al.* (Eds.), Manual of Nearctic Diptera, Volume 1, with permission of the Minister of Supply and Services Canada)


spmth
gen fk
hyp vlv
an lb
an lb
a
b
cerc

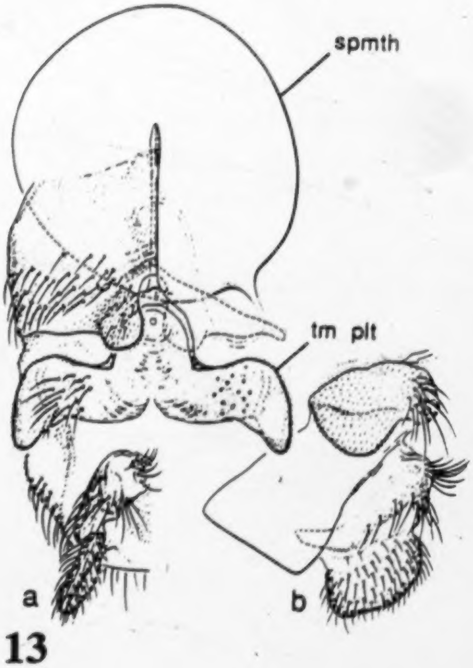
10


spmth
a
b

11


gen fk
arm gen fk
tm plt
st 10
a
b

12


spmth
tm plt
a
b

13

Figures 14 - 16. Female and male terminalia: female terminalia (a , ventral view with left hypogynial valve removed; b, right lateral view at right angles to plane of ventral view) of (14) *Twinnia tibblesi* Stone & Jamnback and (15) *Gymnopais holopticus* Stone; (16) male terminalia (a, ventral view with left gonocoxite and gonostylus removed; b, left lateral view of ventral plate, median sclerite, paramere, and aedeagal membrane; c, terminal (end) view of same structures; d, dorsal (inner) view or right gonosylus) of *Prosimulium mixtum* Syme & Davies.

Abbreviations: an lb = anal lobe; cerc = cercus; gonst = gonostylus; pm = paramere; spmth = spermatheca; stp lk conn = strap-like connection; tm plt = terminal plate; v plt = ventral plate.

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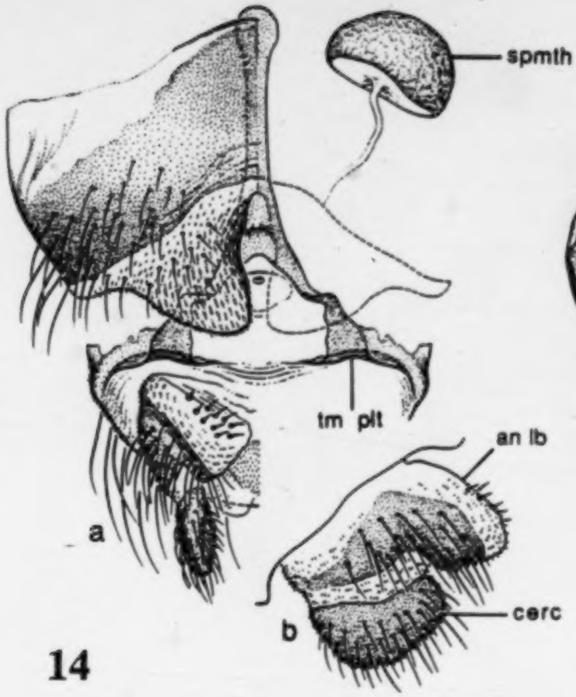
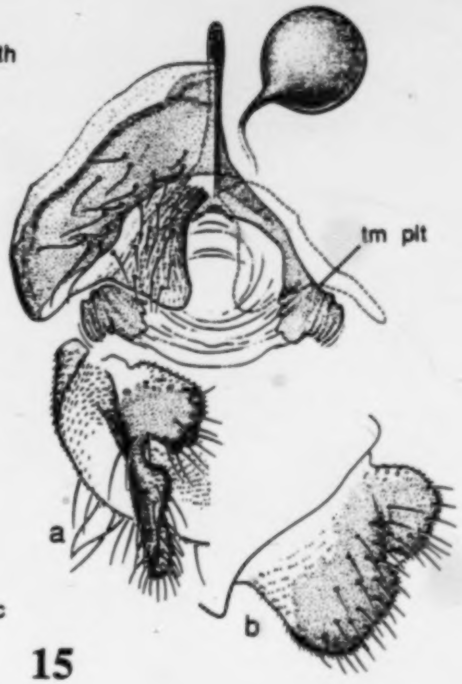
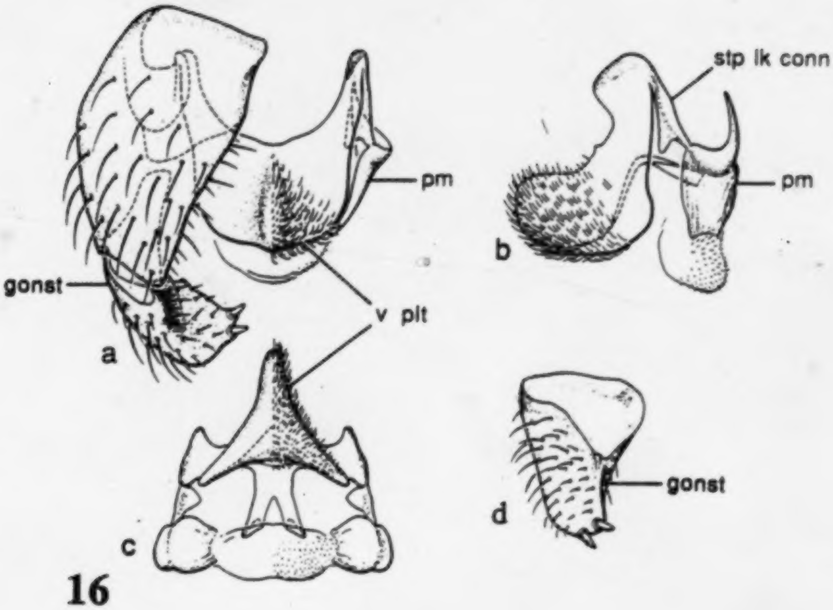

spmth
tm plt
an lb
cerc
a
b

14


tm plt
a
b

15


stp lk conn
pm
pm
gonst
v plt
gonst
a
b
c
d

16

Figures 17 - 18. Male terminalia (a, ventral view with left gonocoxite and gonostylus removed; b, left lateral view of ventral plate, median sclerite, paramere, and aedeagal membrane; c, terminal (end) view of same structures; d, dorsal (inner) view or right gonosylus) of (17) *Helodon* (*Helodon*) *onychodactylus* (Dyar & Shannon) complex and (18) *H.* (*Parahelodon*) *decemarticulatus* (Twinn).

Abbreviations: ant lat apd = anterolateral apodeme; m scl = median sclerite; pm = paramere; stp lk conn = strap-like connection; v plt = ventral plate.

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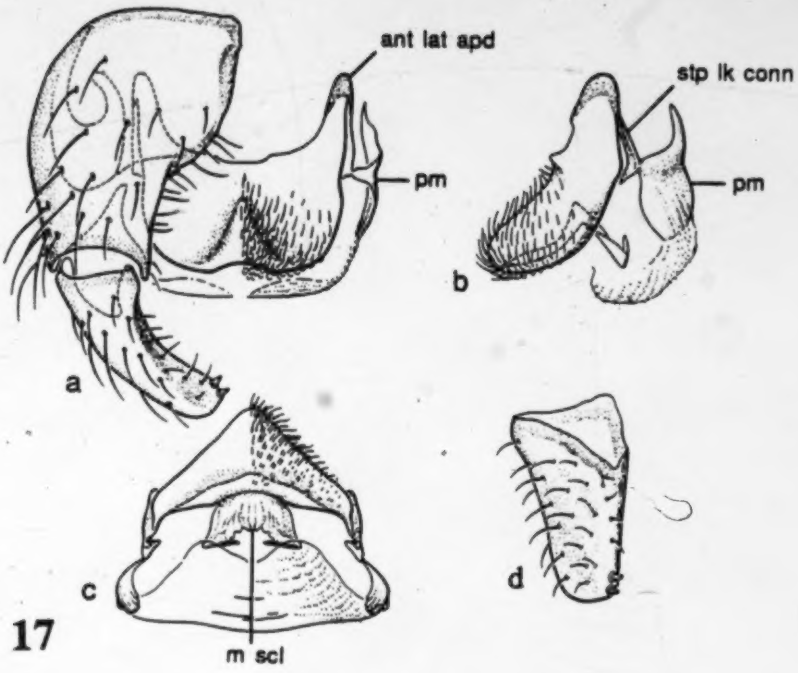
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pm
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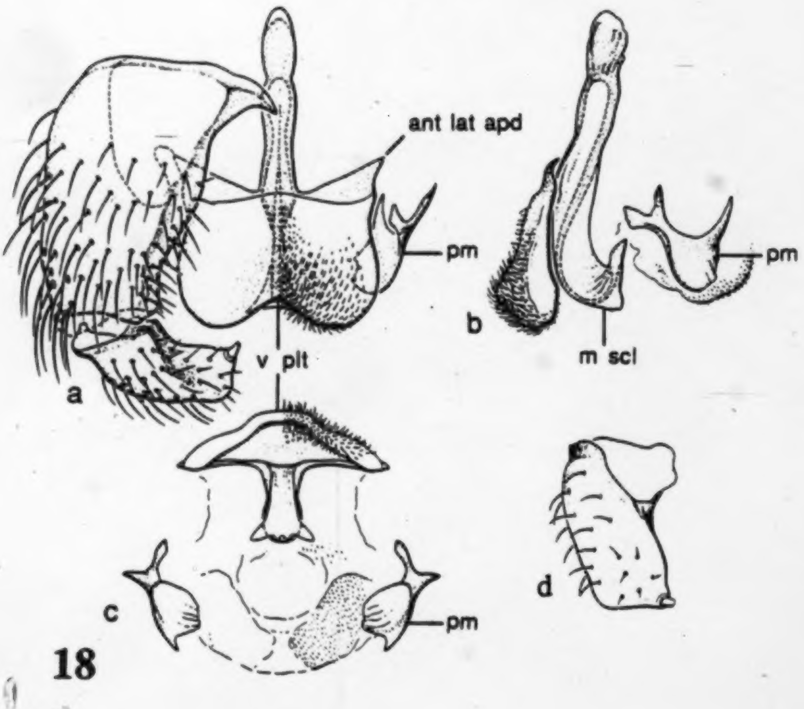
m scl

17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18

Figures 19 - 21. Male terminalia: (19) *Helodon* (*Distosimulium*) *pleuralis* (Malloch) (lateral view); (20) *H.* (*D.*) *pleuralis* (a, ventral view with left gonocoxite and gonostylus removed; b, left lateral view of ventral plate, median sclerite, paramere, and aedeagal membrane; c, terminal (end) view of same structures); (21) *Twinnia tibblesi* Stone & Jamnback (a, ventral view with left gonocoxite and gonostylus removed; b, left lateral view of ventral plate, median sclerite, paramere, and aedeagal membrane; c, terminal (end) view of same structures; d, dorsal (inner) view of right gonosylus).

Abbreviations: ant lat apd = anterolateral apodeme; gonst = gonostylus; m scl = median sclerite; pm = paramere; v plt = ventral plate.

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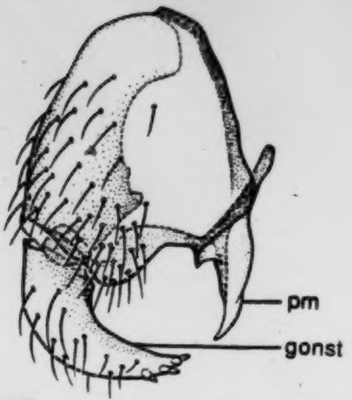
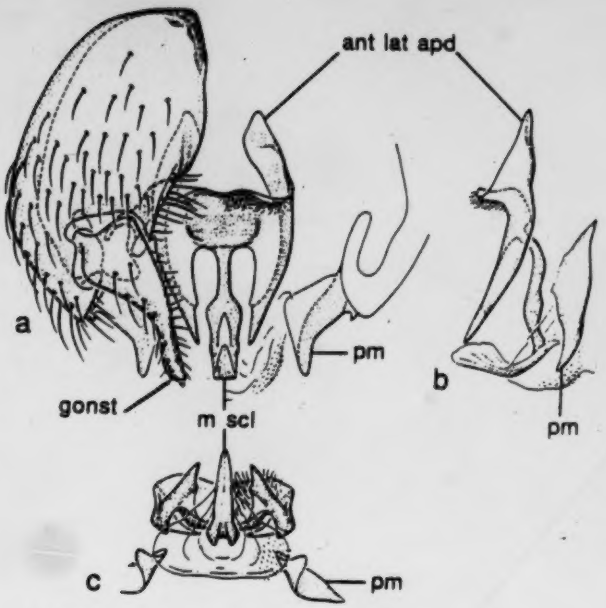

pm
gonst

19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a
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b
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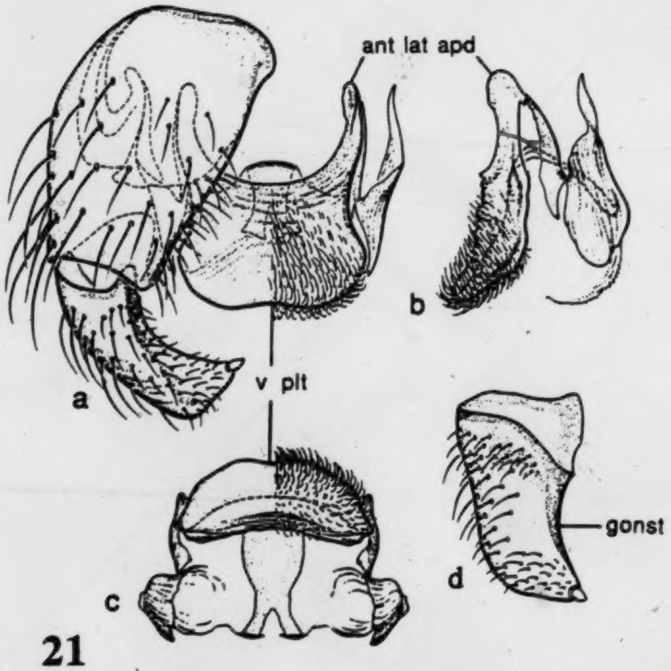
m scl
c
pm

20


ant lat apd
a
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v plt
c
d
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21

Figures 22 - 29. Structural features of the adult and pupa: (22) male terminalia of *Gymnopais dichopticus* Stone (a, ventral view with left gonocoxite and gonostylus removed; b, left lateral view of ventral plate, median sclerite, paramere, and aedeagal membrane; c, terminal (end) view of same structures; (23) head of adult female of *G. dichopticus* Stone (lateral view of left side); (24) thorax of female of *G. holopticus* Stone (lateral view of left side); (25) scutellum and postnotum of female of *G. holopticus* Stone (dorsal view); (26) hind tarsus and claw of female of *Prosimulium ursinum* (Edwards); (27) hind tarsal claw of female of *Helodon* (*Parahelodon*) *decemarticulatus* (Twinn); (28) pupal thorax and gill of *Gymnopais dichopticoides* Wood (dorsolateral view); (29) pupal thorax and gill of *Twinnia nova* (Dyar and Shannon) (lateral view).

Abbreviations: anepst memb = anepisternal membrane; b tth = basal tooth; gonst = gonostylus; mepm tft = mesepimeral tuft; pn = postnotum; sctl = scutellum; stm bul = stemmatic bulla; t clw = tarsal claw; v plt = ventral plate.

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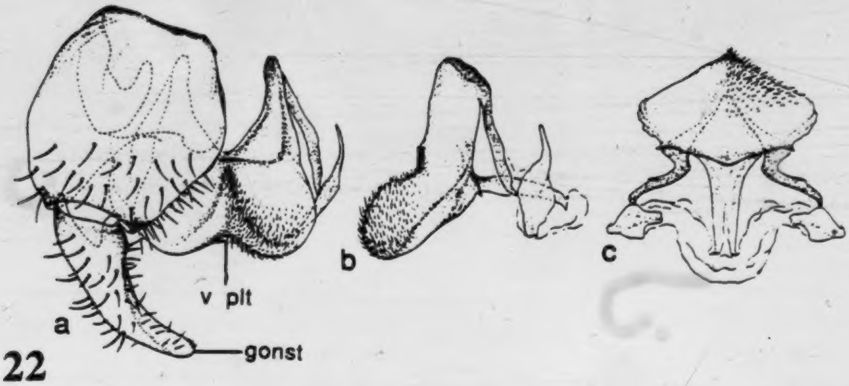
Manual of Nearctic Diptera, Volume 1, with permission of the Minister
of Supply and Services Canada)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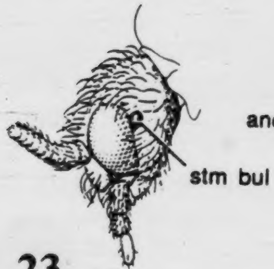
a
b
c
v plt
gonst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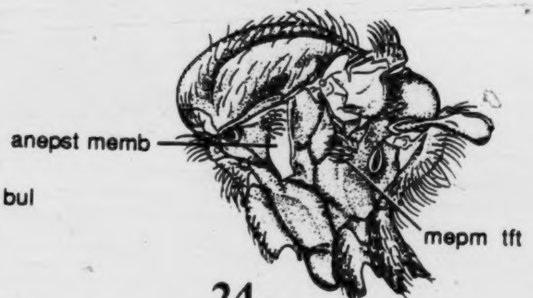
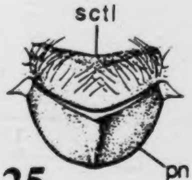

24
anepst memb
mepm tft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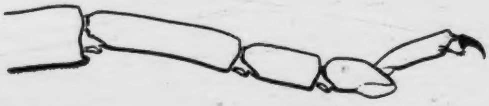
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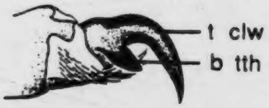
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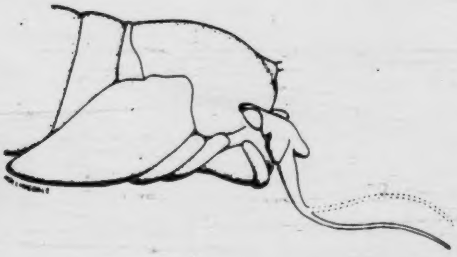
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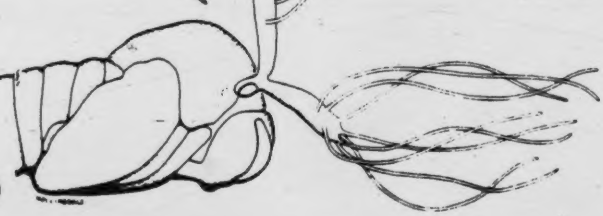
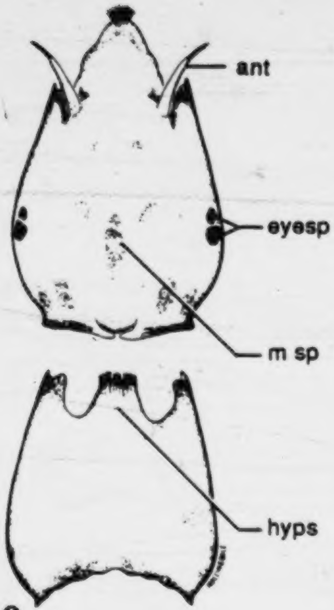
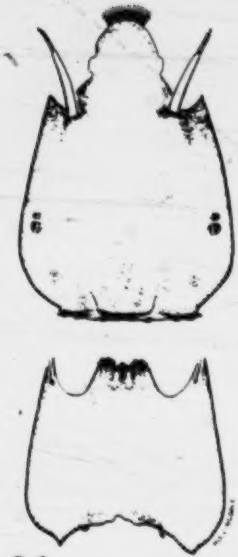

29

Figures 30 - 34. Larval head capsules (upper, dorsal view; lower, ventral view): (30) *Twinnia nova* (Dyar & Shannon); (31) *Gymnopais dichopticoides* Wood; (32) *Helodon* (*Distosimulium*) *pleuralis* (Malloch); (33) *H*. (*Helodon*) *albertensis* (Peterson & Depner); (34) *H*. (*Parahelodon*) *decemarticulatus* (Twinn).

Abbreviations: ant = antenna; eyesp = eyespots; labr fn = labral fan; m sp = median spots; pg clft = postgenal cleft.


ant
eyesp
m sp
hyps

30



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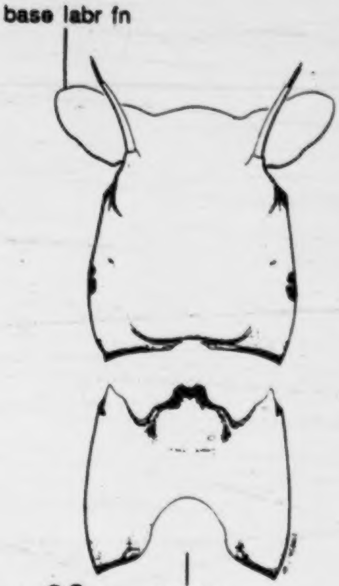
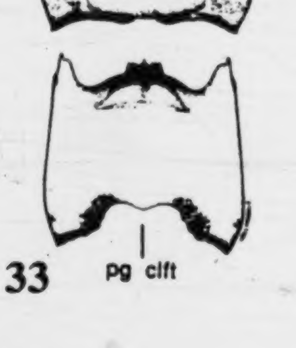

base labr fn
pg clft

32



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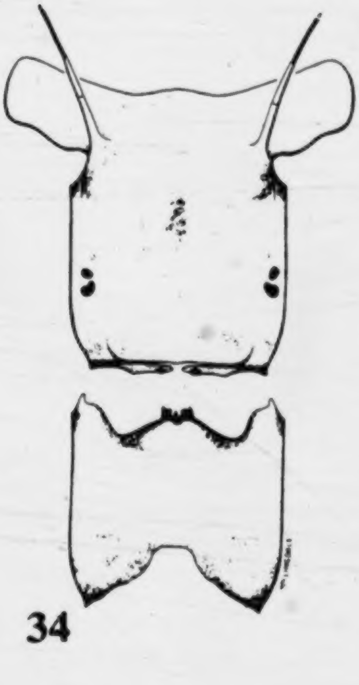
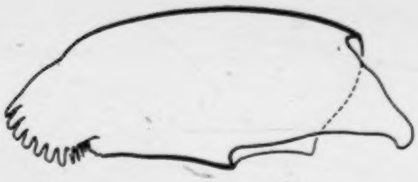


34

Figures 35 - 41. Mouthparts and thoracic features of larvae: (35) left mandible of *Twinnia* (ventral view); (36) left mandible of *Gymnopais* (ventral view); (37) hypostoma of *Helodon* (*Helodon*) (ventral view); (38) hypostoma of *H.* (*Parahelodon*) (ventral view); (39) hypostoma of *H.* (*Distosimulium*) (ventral view); (40) prothoracic proleg of *H.* (*Helodon*) (lateral view of right side); (41) prothoracic proleg of *Prosimulium* (lateral view of right side).

Abbreviations: l plt prlg = lateral plate of proleg; l tth = lateral tooth; m tth = median tooth; sbl tth = sublateral tooth.



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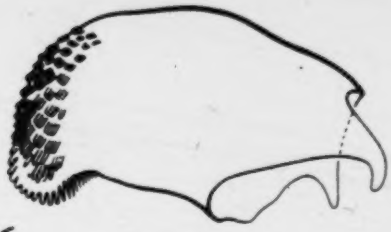

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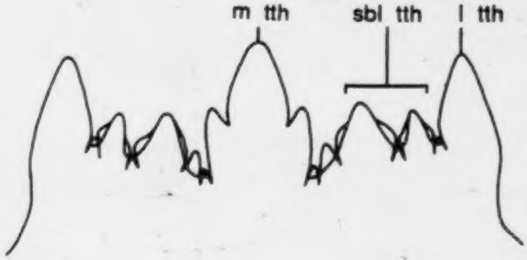
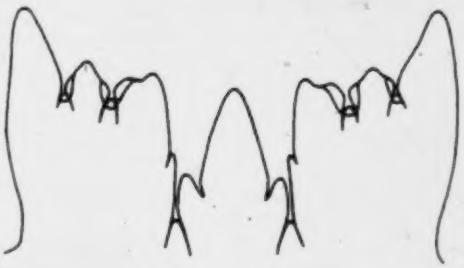

m tth
sbl tth
l tth

37



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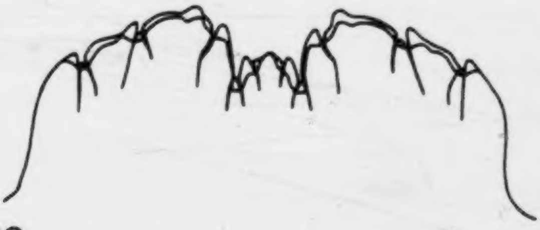

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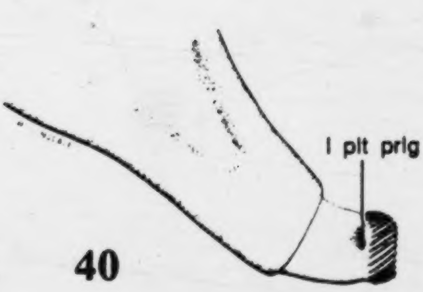

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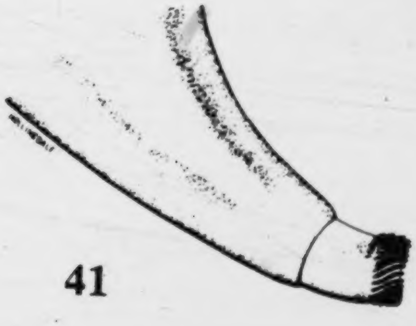

41

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3.11 Appendix I

Checklist of the world species of Prosimuliini: asterisk denotes species examined; list complete to mid-1985, as checked against Crosskey's (1987) checklist of the world species of Simuliidae. Genera and subgenera are arranged phylogenetically, with consitituent species arranged alphabetically. Synonymies are those of Crosskey (*loc. cit.*). Unplaced species are either known only from one or two life-stages, or are not described in sufficient detail to render an informed decision.

Family SIMULIIDAE Newman, 1843
Subfamily SIMULIINAE Newman, 1843
Tribe PROSIMULIINI Roubaud, 1906
    HELLICHIINI Enderlein, 1925
    GYMNOPAIDINAE Rubtsov, 1955
    HELODONTINI [*sic*] Ono, 1982

Genus ***Helodon*** Enderlein, 1921
  Subgenus HELODON s.str.
    albertensis (Peterson & Depner, 1972). **Comb.n.***
    alpestris (Dorogostaisky, Rubtsov & Vlasenko, 1935). **Comb.n.***
      altaicus (Rubtsov, 1956) (subspecies). **Comb.n.**
      relensis (Rubtsov, 1956) (subspecies). **Comb.n.**
      komandorensis (Rubtsov, 1971) (subspecies). **Comb.n.**
    buturlini (Rubtsov, 1956). **Comb.n.**
    chechciri Popov, 1977. **Comb.n.**
    clavatus Peterson, 1970. **Comb.n.***
    czenkanowskii (Rubtsov, 1956). **Comb.n.**
    irkutensis (Rubtsov, 1956). **Comb.n.**
    kamtshaticus (Rubtsov, 1940). **Comb.n.**
    kamui (Uemoto & Okazawa, 1980). **Comb.n.**
    laamii (Beaucournu-Saguez & Bailly-Choumara, 1981). **Comb.n.**
    martini (Peterson, 1970). **Comb.n.***

maruashvili (Machavariani, 1966). **Comb.n.**
multicaulis Popov, 1968. **Comb.n.**
onychodactylus Dyar & Shannon, 1927 (complex). **Comb.n.***
perspicuus Sommerman, 1958. **Comb.n.***
rubicundus Rubtsov, 1956
ferrugineus (Wahlberg, 1842)[1]
  rufus (Meigen, 1838)
  borealis (Zetterstedt, 1842)
susanae (Peterson, 1970). **Comb.n.***

Subgenus PARAHELODON Peterson, 1970. **New status** in *Helodon*
decemarticulatus (Twinn, 1936) (complex). **Comb.n.***
gibsoni (Twinn, 1936) (complex). **Comb.n.***
vernalis (Shewell, 1952). **Comb.n.***

Subgenus DISTOSIMULIUM Peterson, 1970. **New status** in *Helodon*
daisetesensis (Uemoto, Okazawa & Onishi, 1976). **Comb.n.**
pleuralis (Malloch, 1914) (complex)*
  tenuicalx (Enderlein, 1925)
  pancerastes (Dyar & Shannon, 1927)

Genus ***Urosimulium*** Contini, 1963
aculeatum (Rivosecchi, 1963)*
  stefanii Contini, 1963
faurei (Bernard, Grenier & Bailly-Choumara, 1972). **Comb.n.**
juccii Contini, 1966

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[1] Under the plenary powers of the International Commision on Zoological Nomenclature, the specific name *ferruginea* Wahlberg, 1844, as published in the binomen *Simulia ferruginea*, is given precedence over the specific names *rufa* Meigen, as published in the binomen *Simulia rufa*, and *borealis* Zetterstedt, 1842, as published in the binomen *Simulia borealis*, whenever these names are considered synonyms of *ferruginea* (Opinion 1496; 1988, *Bulletin of Zoological Nomenclature* **45**(2): 173-174).

Genus ***Levitinia*** Chubareva & Petrova, 1981
  tacobi Chubareva & Petrova, 1981
  freidbergi Beaucournu-Saguez & Braverman, 1987*

Genus ***Gymnopais*** Stone, 1949
  andrei Vorobets, 1984
  bifistulatus Rubtsov, 1955*
  dichopticoides Wood, 1978*
  dichopticus Stone, 1949*
  fimbriatus Wood, 1978*
  frontatus Yankovsky, 1982*
  holopticoides Wood, 1978*
  holopticus Stone, 1949*
  lindneri Rubtsov, 1963*
  rubzovi Bobrova, 1967*
  sexcornutus Bodrova, 1975
  trifistulatus Rubtsov, 1955*

Genus ***Twinnia*** Stone & Jamnback, 1955
  cannibora Ono, 1977
  hirticornis Wood, 1978*
  hydroides (Novák, 1956)*
  japonensis Rubtsov, 1960
  magadensis Rubtsov, 1973
  nova (Dyar & Shannon, 1927)*
    biclavata Shewell, 1959
  sedecimfistulata (Rubtsov, 1955)*
  subtibbelesi [sic] Ono, 1980
  tatrensis Novák, 1959
  tibblesi Stone & Jamnback, 1955*

Genus ***Prosimulium*** Roubaud, 1906
  albense Rivosecchi, 1961
    silana Rivosecchi, 1967 (unavailable)
  apoina Ono, 1977

approximatum Peterson, 1970
arshanense Rubtsov, 1956
arvum Adler & Kim, 1985*
calabrum Rivosecchi, 1966
candicans Rubtsov, 1956
caudatum Shewell, 1959*
constrictistylum Peterson, 1970*
daviesi Peterson & DeFoliart, 1960*
dicentum Dyar & Shannon, 1927
dicum Dyar & Shannon, 1927*
diminutum Rubtsov, 1956
doveri Sommerman, 1962 (complex)*
erythronotum Rubtsov, 1956
esselbaughi Sommerman, 1964*
exigens Dyar & Shannon, 1927*
  hardyi (Stains & Knowlton, 1940)
flaviantennus (Stains & Knowlton, 1940)
fontanum Syme & Davies, 1958
formosum Shewell, 1959*
frohnei Sommerman, 1958*
frontatum Terteryan, 1956
  stenopalpe Rubtsov, 1956
fulvipes (Edwards, 1921)
fulvithorax Shewell, 1959*
fulvum (Coquillett, 1902)*
fuscum Syme & Davies, 1958*
gigas Rubtsov, 1956
hirtipes (Fries, 1824) (complex)
  sibiricum (Enderlein, 1930)
impostor Peterson, 1970*
irritans Rubtsov, 1940
isos Rubtsov, 1956
italicum Rivosecchi, 1967
jezonicum (Matsumura, 1931)
  sapporoense (Shiraki, 1935)

kanii Uemoto, Onishi & Orii, 1973
karibaense Ono, 1980
kiotoense Shiraki, 1935
kolymense Patrusheva
latimucro (Enderlein, 1925)
    inflatum Davies, 1957
    goidanichi Rubtsov, 1964
longilobum Peterson & DeFoliart, 1960*
luganicum Rubtsov, 1956
macropyga (Lundström, 1911)
    latifrons (Enderlein, 1925)
    ventosum Rubtsov, 1956 (subspecies)
    zaitzevi Rubtsov, 1956 (subspecies)
    arcticum Rubtsov & Carlsson, 1965 (subspecies)
    korshunovi Patrusheva, 1975 (subspecies)
magnum Dyar & Shannon, 1927
    frisoni (Dyar & Shannon, 1927)
    albionense Rothfels, 1956
mixtum Syme & Davies, 1958 (complex)*
multidentatum (Twinn, 1936)*
mysticum Peterson, 1970
neomacropyga Peterson, 1970*
oligoaristatum Rubtsov, 1971
pecticrassum Rubtsov, 1956
petrosum Rubtsov, 1955
    nigritum Rubtsov, 1956 (subspecies)
pronevitschae Rubtsov, 1955
    rachiliense Dzhafarov, 1954
rhizophorum Stone & Jamnback, 1955*
rufipes (Meigen, 1830)
    gallii (Edwards, 1921)
    conistylum Rubtsov, 1956
    aestivale Knoz, 1963 (unavailable)
saltus Stone & Jamnback, 1955
sarurense Ono, 1976

shewelli Peterson & DeFoliart, 1960*
subrufipes Knox, 1980
tomosvaryi (Enderlein, 1921)
    picipes (Stephens, 1829) (nomen nudum)
    fuscipes (von Roser, 1840)
    nigripes Enderlein, 1925
    pexifrons Enderlein, 1925
    balcanicum Enderlein, 1925
    canbalicum (Smart, 1944)
    pseudohirtipes (Smart, 1944)
    arvernense Grenier, 1947
    duodecimfiliatum Rubtsov, 1955
transbrachium Adler & Kim, 1985
travisi Stone, 1952*
tredecimfistulatum Rubtsov, 1956
tridentatum Rubtsov, 1940
uinta Peterson & DeFoliart, 1960
unicum (Twinn, 1938)
ursinum (Edwards, 1935) (complex)*
    browni (Twinn, 1936)
woodorum Peterson, 1970*
yezoense Shiraki, 1935
    alpium Ogata, 1956 (unavailable)

Unplaced species

aridum Rubtzov, 1971 (*Helodon s.str.* ?)
intercalare Rubtsov, 1956
jacuticum Rubtsov, 1973
mesenevi Patrusheva, 1975
pamiricum Chubareva & Petrova, 1983
phytophagum, Rubtsov, 1976 (*Helodon s.str.* ?)
unispinum Rubtsov, 1967

4. CONCLUSION

I have attemped to show that most present-day classifications of Simuliidae are organized into systems of A and not-A categories, and therefore do not reflect accurately phylogenetic relationships. Systematic research on black flies is in an enviable position, in that phylogenetic information is derived from a variety of independent sources (cladistics, cytotaxonomy, chemotaxonomy). As relationships become better understood, there is growing dissatisfaction with the unnatural classifications presently in use. If the various levels of investigation accurately resolve relationships, it should be possible to arrive at the same conclusions, and to derive a uniform and rational classification that serves the needs of all students of the family (whether they be a systematist, cytolologist, physiologist, ecologist, or applied entomologist). The process of classifying is still in the domain of the systematist, and it will remain to the systematist to take into account all available types of data.

In order to formulate a phylogenetic framework from which to study Simuliidae, I have begun necessarily at the base. Discovery of the female and immature stages of *Parasimulium* Malloch made possible resolution of the initial two dichotomies of Simuliidae, which in turn provided the basis for a reclassification at the suprageneric level. Using this as a starting point, I offered an initial interpretation about monophyly and relationships among genus-group taxa of Prosimuliini. A classification that accurately reflected hypothesized relationships among genus-group taxa was proposed.

This work is not intended as the "complete" or "final" word on relationships among primitive black flies. The value of a phylogentic approach to systematics is testability — hypotheses of relationship can be corroborated or falsified by additional information. This is not to suggest that a new classification should be proposed with each new hypothesis.

However, a more rigourous approach to systematics will eventully lead to a better understanding of phylogenetic relationships, and this will ultimately lead to a stable classification. I have attempted to outline areas that require further clarification, though it is doubtful that major modifications will be necessary in the classifaction proposed. Independent sources of information, such as published cytological transformation series, have corroborated many of the hypothesized relationships.

In addition to bringing simuliid classification more into line with current views about phylogenetic relationships, there are other benefits to this approach as well. Many suprageneric names have evidently been created without clear understanding about the relationships of the group under consideration, or the ramifications of recognizing such groups at high taxonomic rank. I take an example from the tribe Prosimuliini to illustrate my point. Ono (1982) recognized the tribe Helodontini, and designated *Helodon* Enderlein as the genotype. If we are to accept this proposal, then it is clear that the rank of other Prosimuliini (as defined in the present work) will have to be adjusted to accomodate this new tribe (cf. fig. 3 of chapter 3). Because *Distosimulium* and *Parahelodon* share a close relationship with *Helodon*, they should be ranked at the same taxonomic (tribal) level. These three tribes together could then be ranked at the subfamily level. In order to balance the classification, a separate subfamily would have to be recognized for each of the remaining genus-group taxa, and this entire assemblage could then be designated a new family! The inappropriateness of Helodontini is immediately realized when phylogenetic relationships are understood.

Although this is an extreme example of a nonsensical ranking, it is equally tempting to create genus-group names without regard to the phylogenetic position of the group under consideration. Crosskey (1987a) drew attention to an alarming trend in the cumulative number of erected supraspecific names since *Simulium* Latreille was first divided. If a balanced classification of Simuliidae is to be achieved, it is no longer acceptable to adopt a strictly phenetic approach to ranking. Splitting at the generic and subgeneric levels is rampant in Simuliidae, and I suggest there there are already more than enough names available to fully classify the family. I advocate greater use of the "species-group" category when phylogenetic relationships remain uncertain.

Some may regard my proposals as radical — that I am tampering with classificatory systems that have long served the every-day practical needs of black fly workers (taxa definition, identification, information storage-and-retrieval). The key word here is systems. There are presently as many views about classification as there are systematists. It is perhaps fortunate that only two world classifications have been proposed during the past 15 years (Rubtsov 1974; Crosskey 1981, 1987b), and that the majority of workers have adopted one or the other. Nevertheless, it is difficult for North American specialists to fully comprehend the Eastern European literature, and *vice versa*. It is hoped that the present work will bridge the gap between the two classifications, and provide a fresh basis from which to view the evolutionary and geographical history of Simuliidae. In addition to testing the ideas presented in the present work, the real need is to resolve phylogenetic relationships within Simuliini. Only then can an informative and stable classification of Simuliidae be achieved.

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